Dakota Skipper (*Hesperia dacotae*)
Report on the Species Status Assessment
Version 2 - September 2018

Photo: Phil Delphey

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Suggested Reference

U.S. Fish and Wildlife Service. 2018. Species status assessment report for the Dakota skipper (*Hesperia dacotae*). 97 pp.

Executive Summary

U.S. Fish and Wildlife Service (Service) developed a species status assessment (SSA) for the Dakota skipper (*Hesperia dacotae*), which was listed as threatened under the Endangered Species Act in 2014. The SSA process is intended to assess the viability of the species using the conservation biology principles 'the 3Rs' – resiliency, representation, and redundancy. We used the SSA analyses to provide a scientific basis for developing the recovery plan for Dakota skipper. In this report we provide a summary of the species' biology at the individual, population, and species levels; describe the factors that have led to its current status and those that are likely to influence its status into the future; assess the current and future health of individual populations given these influences; and describe the implications of predicted health and distribution on the 3Rs.

The Dakota skipper inhabits remnants of tallgrass prairie and mixed-grass prairie in the north-central U.S. and into southern Saskatchewan and Manitoba Provinces of Canada. Within the native prairie patches where it persists, the species relies on high quality habitat conditions – diverse native grassland plant communities – and on natural or human disturbances that maintain the integrity of these plant communities while minimizing mortality to vulnerable life stages. Populations may also be positively or negatively influenced significantly at local, landscape, regional, and continental scales by other factors that include activities such as grazing, haying, burning, pesticide use, and climate change.

To evaluate the degree to which the Dakota skipper may be able to adapt to novel changes in its environment (representation), we delineated areas with potential sources of unique adaptive diversity (referred to as 'adaptive capacity units', ACU). We evaluated the Dakota skipper historical, current, and future distribution within the ACUs to assess the degree of genetic and environmental diversity that the species may have lost to date and is predicted to lose into the future.

As with many species, we were forced to infer some aspects of the species' historical distribution and population dynamics due to an incomplete record of its occurrence before massive conversion of its habitat took place. At locations where its observation was recorded – between the early 1900s and 2017 – the species is gone from about half of the sites. Proximate causes of its local extinction include the complete removal of its native prairie habitat and its replacement with row-crop agriculture, habitat degradation due to recurring intensive livestock grazing and invasive plant species, and unsustainable mortality caused by prescribed fire and insecticide use. The Dakota skipper is now extirpated entirely from one ACU, and in the remaining four ACUs where it has persisted, 17% to 64% of the metapopulations have been lost.

To assess the health of Dakota skipper populations within and among ACUs and, ultimately, the species' viability, we assumed a classical metapopulation structure for the species. Relative to historical conditions, the species' distribution is now fragmented among discrete remnants of native tallgrass and mixed-grass prairie and has been extirpated from major portions of its range, especially in the south and east. Using input from several species experts, we developed a Bayesian Belief Network model to allow us to estimate the likelihood population persistence over 10 years. The key variables, which were identified by expert input, included: (1)

management practices (burning, haying, grazing regimes); (2) pesticide use; (3) habitat patch size; and, (4) current population size. The model uses the effects that these factors would have on Dakota skipper populations – based on the expert opinion – and on our understanding of the current state of each factor and the likely condition of each factor over the next 10 years to predict the probability of persistence in 20 years. We estimated probability of persistence for each subpopulation under a range of plausible future scenarios for the state conditions: the best-case, worst-case, and the most likely-case scenarios.

Under current state conditions, the predicted probabilities of persistence were low, generally – less than 0.5 for more 56% of extant metapopulations – and may be even lower if dispersal among subpopulations is less than we assumed. Under the best-case and worst-case future scenarios, 72% and 63% show no change in the probability of persistence, respectively. That is, populations in poor condition now were likely to have a similar poor health in 20 years. Our model assumed that dispersal would occur in metapopulations; if, however, dispersal does not occur among subpopulations, the estimated likelihoods of persistence may be lower than presented. More than half (57%) of the nominal metapopulations now consist of only one subpopulation and likely have almost no chance of recovery from a local extirpation.

The Dakota skipper is still widespread and persists in a variety of ecological settings, both of which confer resiliency, redundancy, and representation benefits. The frequency and intensity of droughts, for example, likely vary across the many different ecological settings and landscapes that the species still inhabits. The species' current widespread distribution thus provides some buffer against rangewide-scale catastrophes. Nonetheless, the number, health, and distribution of Dakota skipper populations have declined over time and are projected to continue to decline into the future. With these losses, the ability of the species to withstand normal environmental variation and stochastic disturbances (resiliency), catastrophes (redundancy), and its ability to adapt to novel changes such as diseases and climate (representation) have been diminished.

The status of the Dakota skipper will rely on protection of remaining habitat patches from conversion or degradation; grassland management practices that maintain and restore high quality habitat that facilitates population growth, dispersal, and minimizes inbreeding and other processes deleterious to the maintenance of adaptive capacity; low mortality caused by land management; minimization of threats from factors such as pesticide drift; restoration and maintenance of geographic distribution patterns that ensure that the species maintains its ability to persist in the face of stochastic variations in environmental and to adapt to novel environmental changes. Novel environmental changes may include a shift to wetter and warmer conditions in all or a large portion of the species' range that could increase the threat posed by invasive cool-season grasses.

Of note, we were unable to quantitatively assess the current and future vulnerability of Dakota skipper populations to catastrophes; nor have we fully assessed the implications of climate change. Further, our model was predicated upon several assumptions which in totality likely yield an underestimate of risk. In the synthesis portion of the report, we discuss the key uncertainties that should be addressed to increase our ability to predict population trends and to identify, prioritize, and implement important recovery actions.

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Chapter 1. Introduction, Analytical Framework and Methods

This report summarizes the results of a species status assessment (SSA) conducted for the Dakota skipper (*Hesperia dacotae*). We, the U.S. Fish and Wildlife Service (Service), listed the Dakota skipper as a threatened species on October 24, 2014 (79 FR63672) and designated Critical Habitat (80 FR59248) on October 1, 2015. This SSA will be the biological underpinning of a recovery plan for the Dakota skipper, which will be initiated with our partners upon the completion of the SSA in 2018.

The Service revised its approach to recovery planning in 2016; we refer to this revised process as Recovery Planning and Implementation (RPI) (USFWS, 2016). The primary impetus of RPI is threefold: to reduce the time needed to develop and implement recovery plans, increase recovery plan relevancy over a longer time frame, and add flexibility to recovery plans so they can be revised more quickly. Under RPI, a recovery plan includes the statutorily required elements (i.e., measurable criteria, site-specific management actions, and estimates of time and costs), along with a concise introduction and our strategy for how we plan to achieve species recovery. The RPI recovery plan is informed by a separate Species Status Assessment (SSA), which is the subject of this report; the SSA provides information on the species' life history and ecological requirements and on the factors influencing its viability, which are key to recovery plan development. In addition to the recovery plan, RPI entails developing Recovery Implementation Strategies (RIS) in collaboration with partners; these strategies describe on-the-ground activities needed to achieve recovery and identify specific conservation partners, stakeholders, and others who will implement these activities.

This SSA assesses Dakota skipper viability, which we define as the ability to maintain populations over time. To assess viability, we apply the conservation biology principles of resiliency, representation, and redundancy (Shaffer and Stein 2000, pp. 308-311). These principles are generally explained in this chapter and, as they apply specifically to Dakota skipper, in Chapter 2. The remainder of this chapter describes the analytical framework and methods used in completing the Dakota skipper SSA. Chapter 2 summarizes the ecological requirements for survival and reproduction at the individual, population, and species levels. Chapters 3 through 6 summarize the historical, current and predicted future conditions of Dakota skipper and describes the factors that contributed to its current and future status. Lastly, Chapter 7 synthesizes the results from the preceding analyses to describe Dakota skipper viability over time. In this chapter, we also describe sources of uncertainty and their implications.

1.1 Analytical Framework of the SSA

To assess Dakota skipper viability over time, we took the following steps:

1. Described the ecological requirements at the individual, population, and species levels (Chapter 2);
2. Determined the historical condition of Dakota skipper in terms of the number and distribution of healthy populations (Chapter 3);
3. Assessed the current condition of Dakota skipper by describing the number, health, and distribution of currently extant populations (Chapter 4);

4. Described the positive and negative influences that have led to the species' current condition and identified the potential events that could cause catastrophic losses (Chapter 5);
5. Predicted the future state of the influences and devised composite plausible future scenarios (Chapter 6);
6. Assessed the future condition by describing the forecasted health of Dakota skipper populations given the predicted future scenarios (Chapter 6);
7. Evaluated how the change in the number, health, and distribution influence the viability of Dakota skipper over time (Chapter 7).

We use the conservation biology principles of resiliency, redundancy, and representation (Shaffer and Stein 2000, pp. 308-311) to characterize the viability of Dakota skipper. To sustain populations over time, a species must have a sufficient number and distribution of healthy populations to withstand:

(1) Annual variation in its environment (Resiliency);
(2) Catastrophes (Redundancy); and,
(3) Novel changes in its biological and physical environment (Representation).

Viability is a continuous measure of the likelihood that the species will sustain populations over a specified time period and can be defined in relative terms, such as "low" or "high" viability. A species with a high degree of resiliency, representation, and redundancy is generally better able to adapt to future changes and to tolerate stressors (factors that cause a negative effect to a species or its habitat), and thus, typically has a high viability.

Resiliency means having populations robust to environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature, rainfall, etc.), periodic disturbances (e.g., fire, floods, storms), and anthropogenic stressors (Redford et al. 2011, p. 40). Simply stated, resiliency refers to a species' ability to sustain populations through periods of both favorable and unfavorable environmental conditions and/or anthropogenic impacts.

Species resiliency requires having healthy (demographically and genetically robust) populations (adapted from Redford et al. 2011, p. 40-41). Demographically and genetically robust populations have large population sizes and strong growth rates. These two attributes help buffer against genetic, demographic, and environmental stochasticity (Wolf et al. 2015, p. 206). In addition to healthy populations, species' resiliency benefits from having populations distributed across areas with varying environmental conditions (referred to as spatial heterogeneity).

Environmental stochasticity is spatially correlated at regional and local scales (Hanski and Gilpin 1997, p. 372), causing populations to fluctuate in synchrony over broad geographical areas (Kindvall 1996, pp. 207, 212; Oliver et al. 2010, pp. 480-482). Thus, having populations distributed across a diversity of environmental conditions helps guard against concurrent losses of populations by facilitating asynchronous fluctuations among populations. Generally speaking, the more spatial heterogeneity (e.g., the diversity of temperature and precipitation conditions occupied), the more resilient the species will be.

Lastly, resiliency may be influenced by the degree of connectivity among populations, which may be important for genetic health and demographic rescue. Maintaining gene flow among populations promotes genetic diversity (heterozygosity) within populations. Connectivity also provides for supplementing or recolonizing populations that have suffered declines or extirpation due to stochastic events.

Redundancy is the ability of a species to withstand catastrophes; those infrequent but highly consequential events for which adaptation is unlikely. This provides a margin of safety to reduce the risk of losing substantial portions of adaptive diversity or the entire species to a single or series of catastrophes (USFWS and NOAA 2014, p. 37578). Redundancy is best achieved by having multiple populations widely distributed across the species' range, thereby reducing the likelihood that all populations are exposed simultaneously to the effects of catastrophic events. In short, redundancy is about spreading the risk. Redundancy is essential for long-term viability (Shaffer and Stein 2000, pp. 307, 309-310; Groves et al. 2002, p. 506).

Representation is the ability of a species to adapt to both near-term and long-term novel changes in the physical (e.g., climate or habitat) and biological (e.g., novel diseases, pathogens, predators) conditions of its environment. Simply stated, representation is the evolutionary or adaptive capacity of the species (Beever et al. 2016, p. 132; Nicotra et al. 2015, p.2), and its ability to persist in the face of multiple, novel threats (Lankau et al. 2011, p. 323). Thus, it is essential for species viability (Lankau et al. 2011, p. 316).

Sources of Adaptive Capacity

Species respond to novel changes in their environment by altering their physical or behavioral traits (phenotypes) to match the new environmental conditions either through plasticity or genetic change (Chevin et al. 2010, p. 2; Hendry et al. 2011, p. 162; Nicotra et al. 2015, p.3). For adaptation to occur, there must be variation upon which to act (Lankau et al. 2011, p. 320). Because phenotypes are determined by genes or sets of genes (genotypes), genetic diversity is crucial for adapting to novel environmental conditions (Hendry et al. 2011, pp. 164-165; Sgro et al. 2011, p.326).

There are two types of intraspecific genetic diversity: adaptive and neutral (Sgro et al. 2011, p. 328; Holderegger et al. 2006, p. 797). Both are important for preserving the adaptive potential of a species (Moritz 2002, p. 243) but in different ways. Adaptive genetic diversity is the variation in traits that control fitness (Holderegger et al. 2006, pp. 801, 803; Lankau et al. 2011, p. 316); thus, it is the variation that underpins evolution (Sgro et al. 2011, p. 328). The more adaptive diversity a species harbors, the more capacity it has to adapt to changing environmental conditions. Adaptive diversity is difficult to measure because evolutionary response is controlled by a complex interaction among multiple traits (Hendry et al. 2011, p. 162; Teplitsky et al. 2014, p. 190) and, most often, involves both plastic and genetic components (Hendry et al. 2011, p.163; Lankau et al. 2011, p. 316). Accordingly, variation in biological characteristics and ecological conditions are used as indicators of adaptive diversity. Variation in biological traits (e.g., physiological, morphological, and life history characteristics, collectively referred to as phenotypic plasticity) will preserve important adaptive traits and their underlying genetic variation (Crandall et al. 2000, p. 291; Forsman 2014, p. 304; Nicotra et al. 2015, p. 3). Maintaining populations across an array of environments (Hoffmann and Sgro 2011, p. 484;

Lankau et al. 2011, p. 320; Sgro et al. 2011, p. 332; Shafer and Stein 2000, p. 308) and on the periphery of its distribution (Ruckelshaus et al. 2002, p.322) helps preserve the breadth of a species' adaptive diversity.

Conversely, neutral genetic diversity is the variation in genotypes that have no direct effect on fitness (Sgro et al. 2011, p. 328) and is easier to measure via molecular-genetic markers (Holderegger et al. 2006, p. 798). This type of genetic diversity arises from historical isolation and gives rise to evolutionary lineages (Moritz 2002, p.239). The evolutionary history of a lineage is important because it influences the phenotypes and genotypes currently present within the species (Hendry et al. 2011, p. 167). The longer the history of isolation, the more likely it is that the populations within each lineage harbor unique genetic variation, including adaptive traits (Hendry et al. 2011, p. 167). Hence, populations that are phylogenetically (molecularly or morphologically) divergent can serve as indicators of underlying adaptive diversity.

Evolutionary Process & Forces

Maintaining the adaptive capacity of a species also requires preserving the processes that allow for evolution to occur (Crandall et al. 2000, p. 290; Sgro et al. 2011, p. 327). The key evolutionary forces are natural selection, gene flow, mutations, and genetic drift (Zackay 2007, p. 1; Crandall et al. 2000, p. 291). Natural selection is the process by which heritable traits can become more (selected for) or less (not selected for) common in a population by favoring those traits that enhance survival (Hendry et al. 2011, p. 169). To preserve natural selection as a functional evolutionary force, it is necessary to maintain populations across the breadth of biological and ecological conditions. Gene flow influences genetic diversity by introducing new alleles into a population, and hence, increasing the gene pool size. Genetic drift influences the frequency of alleles in a population via random, stochastic events. Genetic drift is most influential in isolated populations or those with small effective population sizes (Zackay 2007, p. 4). Preserving genetic connections among populations helps preserve gene flow as an evolutionary process, while maintaining populations with large effective population sizes will keep genetic drift in check (Crandall 2000, p. 293).

1.2 Methods

To assess Dakota skipper viability over time, we: 1) reviewed and assessed survey records from approximately 300 occupied and historically occupied sites between 1905 and 2017 (1905-1911 specimens were identified from vouchers after the species was first described in 1911); 2) defined Dakota skipper population structure and delineated populations; 3) described the species' ecological requirements; 4) assessed the number, health and distribution of all subpopulations and metapopulations; 5) identified the substantive factors leading to the species' current condition and the magnitude, extent, and likely effects of future influences; 6) forecasted the future number, health, and distribution of populations given these influences; and 7) assessed the subsequent change in resiliency, redundancy, and representation over time and the implications for Dakota skipper viability. The general framework for our analysis is depicted in Figure 1.1.

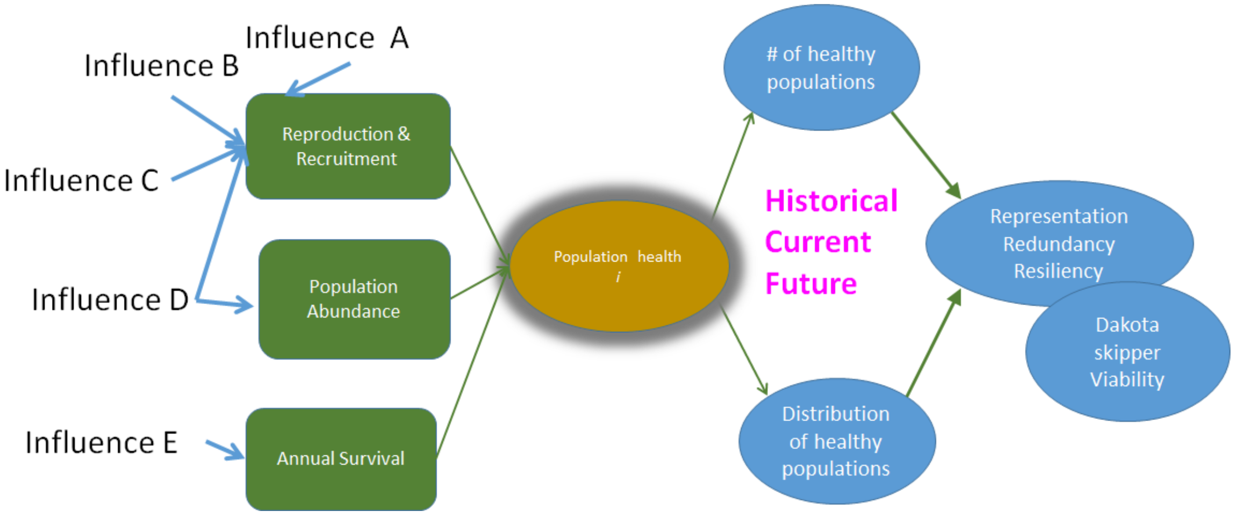


Figure 1.1. General analytical framework to assess Dakota skipper viability over time.

Dakota Skipper Metapopulations

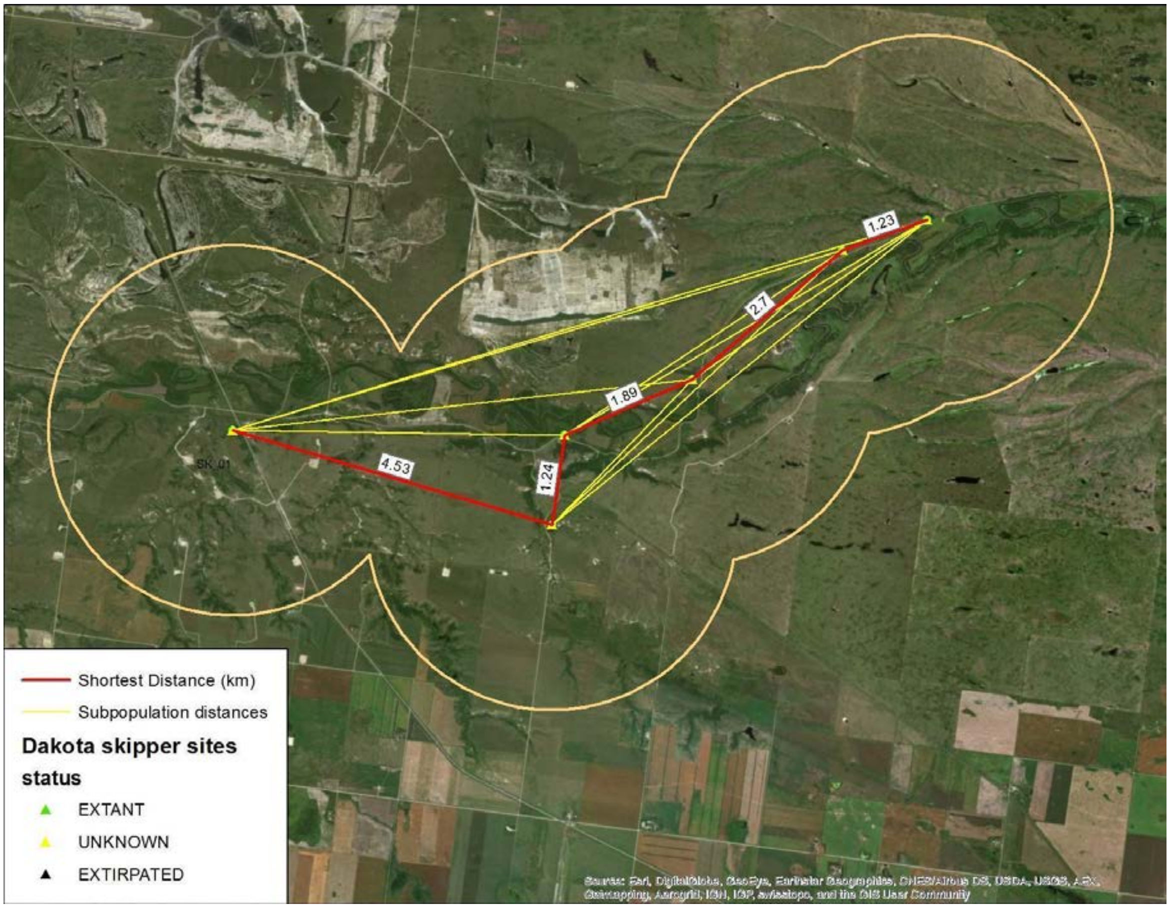
We assessed the status of the Dakota skipper with the assumption that its populations function as classical metapopulations, a model that may approximate how the species' functioned historically. In classical metapopulations, all subpopulations are subject to extirpation and the probability of extirpation is inherently identical but independent (asynchronous) among subpopulations. Recolonization is slow and occurs at a rate that increases when there are more subpopulations. Persistence of the metapopulation depends on the fate of the individual subpopulations, but also on the influence of barriers to dispersal (USFWS 2003, p. E-53).

There is evidence that gene flow occurred at regional scales in the Dakota skipper historically (Britten and Glasford 2002), but this may have occurred over long time frames because adults do not disperse often or over large distances. In addition, the habit of the species to make only short movements during its brief single annual flight period may have resulted in slow recolonization of areas where populations were locally extirpated by natural events, like fire, intense bison grazing, or flooding. The Dakota skipper, like other species, does not fit any conceptual model perfectly, but we determined that for these reasons the classical metapopulation model would fairly characterize the species' historical structure well and that it would be useful model to analyze its current status and future trends.

To identify and delineate metapopulations of the Dakota skipper we used the Service's Dakota skipper geodatabase (USFWS unpublished geodatabase) which consists of two primary sets of data tables, Skipper_all_sites (general information compiled from the entire survey effort) and Skipper_surveys (specific information for each attempted survey). These data tables and geospatial points track and evaluate the survey effort at both known Dakota skipper sites and those areas with potential for suitable habitat, but where Dakota skippers have never been observed. For the purposes of our analysis, only confirmed Dakota skipper observations were used to identify metapopulations boundaries. Of the sites with confirmed Dakota skipper observations, these data tables contain the geographic coordinates and other attribute data associated with over 2,000 surveys conducted at approximately 300 sites where the species was recorded from 1905 to 2017. Surveys tracked in the database were conducted during the species' flight period, under appropriate weather conditions, at the appropriate time of day, and by persons qualified to identify the species. The geographic coordinates associated with each record represent one of the following: 1) the approximate center point of the habitat patch surveyed, 2) the approximate center point of Dakota skipper observations within the surveyed patch, or 3) precise locations of observed Dakota skippers.

Once all the historically occupied and currently occupied subpopulations were identified, the points associated with those records were grouped into metapopulations. Many of those point records do not have enough information to accurately identify boundaries of habitat patches. To address this, we delineated metapopulations based on the average distance between the point locations in the database that represent discrete Dakota skipper sites (habitat patches). As suggested above, the boundaries of the habitat patches contain these points, but the distances between the point locations and the edges of the habitat patches are typically not known precisely.

In light of the uncertainty with regard to the shape and extent of habitat patches that contain each point representative of a local (sub-) population of the Dakota skipper, we assigned subpopulations whose representative points were on average less than 5 km but no more than 6.5 km from one another to the same metapopulation (see Figure 1.2 for illustration). For example, if the average distance among a set of points (subpopulations) was greater than 5 km, the outlying subpopulations were eliminated from consideration as part of the metapopulation, until the average distance among the remaining points was no more than 5 km. For the purposes of this report, isolated populations are counted and referred to as metapopulations although they are so in name only. We clarify the number of populations that fall into this category below, by stating the number of 'metapopulations' that consist actually of only a single discrete population.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 1.2. A group of Dakota skipper subpopulations represented by point locations inside their respective habitat patches. These subpopulations were grouped for analysis into a single metapopulation because the average distance among all points was less than 5 km and no points were further than 6.5 km from another representative point within the metapopulation.

Influences

We searched the published and unpublished literature and queried species experts to identify past and current negative and beneficial factors that have influenced the status of Dakota skipper meta- and subpopulations across its historical range. Factors having a negative impact on Dakota skipper individuals are referred to as risk factors or stressors; whereas factors having a beneficial effect are referred to as supportive factors. We refer to risk and supportive factors collectively as "influences."

We elicited input on the accuracy of our list of influences and the magnitude of impact such influences are likely to have on Dakota skipper status from species experts. We asked the experts to review our list of influences and to identify additional influences. Detailed information about these influences can be found in Chapter 5 of this report.

Number, Health, and Distribution of Populations

We evaluated the number, health, and distribution of Dakota skipper metapopulations for three time-frames: historical, current, and future. To assess the number, health, and distribution for each period, we first defined status categories (Table 1.1). Using these categories, we tallied the number of extant (E), presumed extirpated (PX), extirpated (X), and unknown (UK) populations during historical and current time-periods. For the historical time period, our tally of populations underestimates the species' distribution and abundance because we must rely on an incomplete record of the species' historical distribution. Conversion of Midwestern grasslands began in the 1800s; the species was likely extirpated from large parts of its historical range before the limits of its former distribution were recorded.

Table 1.1. Category definitions for classifying Dakota skipper population status

Dakota Skipper Status Categories	
Extant	Species was detected during the most recent survey within the last ten years and habitat is still present.
Presumed Extirpated	Very degraded habitat with low probability of occurrence or historical record prior to 1975 that are lacking recent survey data.
Extirpated	At least three sequential years of negative surveys or habitat is no longer present.
Unknown	All other scenarios (i.e. species was found more recently, but not in the most recent one to two sequential survey year(s) and there is no evidence to suggest the species is now extirpated from the site).

To assess the health of the metapopulations, we constructed two Bayesian Belief Network models: the first to assess the health of subpopulations and the second to assess the health of the metapopulation to which the subpopulations presumably belongs (Figure 1.3). The output for both models is probability of persistence.

A Bayesian Belief Network consists of nodes, states, links and conditional probability tables (CPT). Nodes are input and response variables, states are the possible conditions of the variable, links establish causal relationship among the variables, and the CPT provide the likelihoods (referred as 'beliefs') of a variable being in one of the possible states. The input nodes represent either the current 'state' or the predicted future 'state' of the variable and the probability that each is in one of the possible states. The values of the response variables are governed by the states of the input nodes that influence the response node. For more information about Bayesian Belief Network modeling, see http://www.norsys.com/tutorials/netica/nt_toc_A.htm.

To construct the model structure and the underlying CPTs, we sought out expert input. Based on butterfly and Dakota skipper-specific biology, we believe Dakota skipper metapopulation persistence is primarily influenced by the health of subpopulation(s), connectivity among the subpopulations, and risk due to catastrophes. Although the experts believe connectivity among the subpopulations influences the probability of metapopulation persistence through both rescue effect and genetic health, they were unable to reliably quantify the causal relationship between the degree of connectivity and metapopulation persistence. Similarly, we were unable to determine a reliable frequency estimate for catastrophic drought. Thus, the metapopulation model is composed of just one variable: probability of at least one subpopulation persisting.

To assess subpopulation health, we constructed a model to predict the probability of persistence of each subpopulation (Figure 1.3). The influences evaluated in the model include four types of habitat management, the overall effect of management on Dakota skipper mortality, the potential risk of flooding, the current abundance, current overall mortality, current habitat conditions, nearby herbicide use, current extent of habitat, and connectivity of habitat patches. More information about these influences is found below and in Chapter 5.

Influence variables included in the Bayesian Belief Network models:

1. Grazing - indirect effects of management regime - that is, how well does grazing at the site support Dakota skipper considering its effects to essential habitat features
2. Haying - indirect effects of management regime - that is, how well does haying at the site support Dakota skipper considering its effects to essential habitat features
3. Herbicide Use - indirect effects of management regime - that is, how well does herbicide use at the site support Dakota skipper considering its effects to essential habitat features
4. Fire - indirect effects of management regime - that is, how well does fire management at the site support Dakota skipper as a result of its effects to essential habitat features
5. Management Effect - direct mortality incurred from haying, grazing, fire and/or insecticide use
6. Hydrology Effect - direct mortality incurred from flooding at the site
7. Current Population Level (N) - the current population size of the subpopulation
8. Current Mortality - the level of mortality occurring from current management and other factors
9. Current Habitat Conditions - quality of current habitat conditions
10. Nearby Herbicide Use - the risk posed by drift of herbicides from nearby agricultural lands
11. Current Extent of Quality Habitat - how extensive is high quality habitat in the area inhabited by the subpopulation
12. Current Connectivity - the average distance between habitat patches within the area inhabited by the subpopulation.

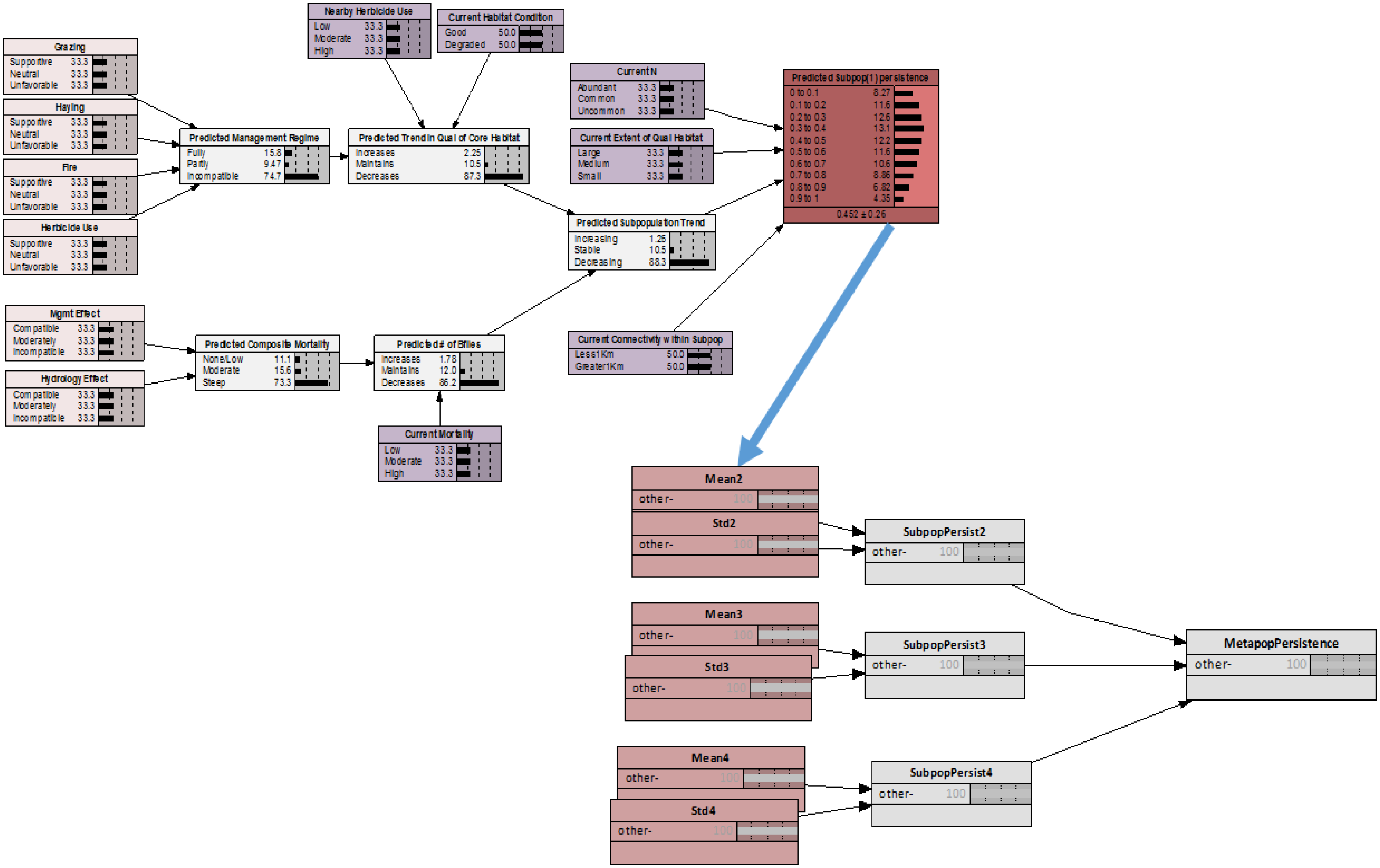


Figure 1.3. Bayesian Belief Network models used to assess the health of Dakota skipper metapopulations.

To populate the models for each meta- and subpopulation, three of the SSA core group members—who possess species' and/or land management expertise and first-hand knowledge at the site--provided the beliefs for the input nodes. We asked them to distribute 100 among the all possible states based on their degree of belief the node is in each state (Figure 1.4). For example, if they believed that grazing was at least neutral for a subpopulation, but believed more strongly that it is supportive, the scores may be 75 for 'supportive', 25 for 'neutral', and 0 for 'unfavorable' state. They completed the exercise for both current conditions, as well as forecasted future conditions. For the forecasted future, we asked them to provide beliefs considering realistic best, worst, and most likely scenarios. Influences 7-12 are current state conditions and are thus held constant for current and future scenarios; influences 1-6 are future state conditions and thus are changed in future scenarios.

When assessing habitat management types that were either not implemented at a site or not anticipated to be implemented, scores were spread evenly among the state conditions (i.e., supportive, neutral, and unfavorable). For example, if we did not expect the habitat for a subpopulation to be hayed, we divided the 100 points evenly among the three state conditions. We also evenly divided the 100 points among state conditions when we did not have reliable information to assign beliefs. For example, we did not have information about the current population level for several subpopulations.

For influences 1-4, the states were defined as:

- Supportive: will maintain or create suitable core habitat
- Neutral: no effect on core habitat or,
- Unfavorable: will not maintain or create suitable core habitat

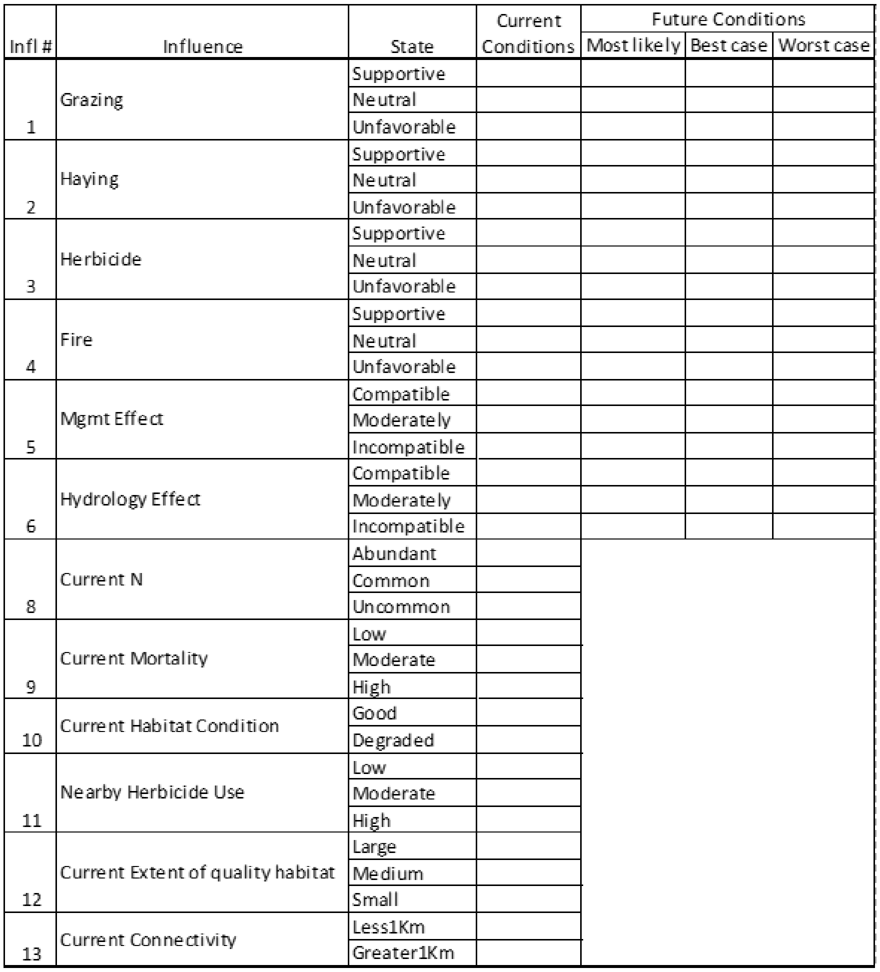
For influence 5, Management Effect, states were defined as,

- Compatible: mortality of individuals may occur but not to the level of affecting subpopulation trend;
- Moderately compatible = mortality of individuals occurs at a level likely to affect a subpopulation trend reduction, but mortality occurs over time and the trend can be reversible;
- Incompatible: mortality of individuals rises to the level that subpopulation trend will be irreversibly reduced.

For Hydrology (influence number 6), we entered our beliefs that flooding would have a low, moderate, or high likelihood of exerting a negative effect on population growth. We did not further define high, medium, and low states for this influence.

For influence 7, if we had data to describe the relative abundance of Dakota skippers at the site, we assigned scores for current population level as follows (thresholds were obtained by expert input, Szymanski et al. 2018): Abundant (≥10/search hour), Common (5-9/search hour), or Uncommon (<5/search hour).

To assign values for nearby herbicide use (influence 10), we relied on distance from row-crop agriculture based on our interpretation of aerial imagery. The method of application, weather, and equipment can affect pesticide drift (USFWS 2017). To avoid drift into non-target areas during aerial spraying, buffers of 600 feet (183 meters) have been “generally recommended”, but buffers of a half mile or more might be needed depending on application measures (USFWS 2017, p. 124). In Dakota skipper habitat high concentrations of insecticides have been documented as far as one kilometer from the edge of a crop field that was aerially sprayed (Runquist and Heimpel 2017, p.8). To account for the potential for aerial application of insecticides immediately adjacent to Dakota skipper habitat - a reasonable worst-case scenario - if any amount of row-crop agriculture was present in the most recent aerial imagery within 750 meters of a subpopulation point location or if herbicide use has been documented as an ongoing or imminent threat at the site, we assigned all points to the state “High”. If row-crop agriculture was present within 750-1500 meters or greater than 1500 meters from a subpopulation point location, the state condition for the subpopulation was “Medium” or “Low”, respectively. Finally, we described the state condition for “Current extent of quality habitat” (influence 9) as Large (>160 acres); Medium (10-160 acres); or, Small (<10 acres). These size classes are smaller than the ranges of prairie remnant sizes for which Swengel and Swengel (1997, pp. 134–137; 1999, p. 284) found no Dakota skippers (less than 49 acres) and relatively low (74–321 acres) and high (greater than 346 acres) relative abundances. A key difference is that we considered the extent of “quality habitat” within remnants whereas they grouped sites based on the entire extent of the prairie remnant, which likely contained some areas that were not habitat for the Dakota skipper (e.g., areas heavily invaded by smooth brome, wetlands, etc.). In addition, the Dakota skipper has been recorded at numerous sites where the extent of habitat was reported to be less than 49 acres.



Infl #	Influence	State	Current Conditions	Future Conditions		
				Most likely	Best case	Worst case
1	Grazing	Supportive				
		Neutral				
		Unfavorable				
2	Haying	Supportive				
		Neutral				
		Unfavorable				
3	Herbicide	Supportive				
		Neutral				
		Unfavorable				
4	Fire	Supportive				
		Neutral				
		Unfavorable				
5	Mgmt Effect	Compatible				
		Moderately				
		Incompatible				
6	Hydrology Effect	Compatible				
		Moderately				
		Incompatible				
8	Current N	Abundant				
		Common				
		Uncommon				
9	Current Mortality	Low				
		Moderate				
		High				
10	Current Habitat Condition	Good				
		Degraded				
11	Nearby Herbicide Use	Low				
		Moderate				
		High				
12	Current Extent of quality habitat	Large				
		Medium				
		Small				
13	Current Connectivity	Less1Km				
		Greater1Km				

Figure 1.4. Table used to gather the input data for the models from SSA team members. For each subpopulation, one SSA team member assigned beliefs for each input node.

Viability over Time

To assess the Dakota skippers' ability to sustain populations over time, we analyzed how the change in number, health, and distribution of populations over time influence the species' resiliency, redundancy, and representation.

<u>Resiliency</u>

To assess the species' ability to sustain populations given normal, year-to-year variations in environmental conditions (e.g., variations in temperature and rainfall) and periodic perturbations (e.g., fire, floods, and storms), we analyzed the trend in the number of healthy populations and the degree of asynchrony among populations over time. We used the Bayesian Belief models explained previously to assess population health (measured by its probability of persistence given influences acting upon it). To assess the degree of population asynchrony, we intended to evaluate the distribution of Dakota skipper across varying environmental conditions (i.e., change in spatial heterogeneity). This analysis would allow us to evaluate the change in Dakota skipper's ability to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature, rainfall, etc.), and periodic disturbances (e.g., fire, floods, storms). Specifically, we evaluated the trend in Dakota skipper occurrence across Bailey's Sections (Bailey 1997) to assess the change in spatial heterogeneity. Sections are subregions of Provinces that are based largely on differences in landforms (Bailey 2004). These variations in landforms may be representative of ecological distinctions that contribute to environmental heterogeneity. Bailey's Sections capture variation in topography across the range of the Dakota skipper and within ACUs. The Bailey's system does not provide further subdivision of its North American Provinces for Canada. Therefore, we used the Ecoregion units that are part of the National Ecological Framework for Canada (http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html) and are similar in scale to Bailey's Sections.

Redundancy

We defined a catastrophe as an event that would cause complete metapopulation failure irrespective of population health. We evaluated several threats that could potentially be catastrophic for Dakota skipper: drought, flooding, large-scale prairie conversion, pesticides (direct application and drift/overspray), land management actions, and disease and parasites. Of these, drought was the only foreseeable catastrophe. Flooding, prairie conversion, pesticide application, and land management actions are all unlikely to occur at the spatial scale that would negatively affect an entire metapopulation. Each of these stressors certainly could affect Dakota skipper at a more local scale, and some are captured in the resiliency analysis. We did not have sufficient information about diseases or parasites to describe the frequency or likelihood of an epizootic.

To assess Dakota skipper vulnerability to catastrophic drought, we intended to map the spatial variation in drought risk and overlay the historical, current, and future distribution of Dakota skipper locations, although, we were unable to complete a quantitative assessment in time for this report (if determined to be important for recovery planning and implementation, we will undertake this analysis at a later date). During a recovery planning workshop (July 2018), the participants identified pesticide response to a widespread pest outbreak as a potential catastrophic event. Although not considered in our analyses to date, it will be addressed in recovery planning moving forward.

Representation

To assess the species' ability to adapt to novel changes in the physical (e.g., climate conditions, habitat conditions or structure across large areas) or biological (e.g., diseases, pathogens, predators) environment, we identified variation in climate and habitat characteristics that could be indicators of underlying adaptive diversity. Using these potential indicators, we spatially partitioned Dakota skipper diversity into geographic units (referred to as adaptive capacity units, ACU). We used the Bailey's Ecoregions of North America model (Bailey 1997) at the Province level as the general construct to map the variation in adaptive capacity across the species' range. We chose this hierarchical level because the provinces are differentiated by features that are relevant to potential major adaptations by the Dakota skipper, such as vegetational macro-features (e.g., including the relative amounts of short-, mid-, and tallgrass prairie), the amount and relative dominance of forest and grassland, and climatic differences (e.g., including the degree of aridity, frequency of drought, and variation in temperature across country boundaries). Bailey (1998) noted “that these ecoclimatic zones are greatly simplified” and that “(T)he actual boundaries may be very irregular.” To this end, we found reason to slightly modify the boundaries in some circumstances. Using knowledge of local areas and input from species experts and land managers, we used the Major Land Resource Areas (NRCS 2006) and Canadian EcoDistricts (ESWG 1995)--both of which take into account soil, terrain, and regional land management-- to make modifications.

The historical distribution of Dakota skipper spans five adaptive capacity units (Figure 1.5) [1]: (1) 332-Dry Steppes, (2) 331-Steppes, (3) 251A- Prairie Parklands - Red River Valley Section, (4) 251B-Prairie Parklands - Prairie Coteau Section, and (5) 221-Broadleaf Forests.

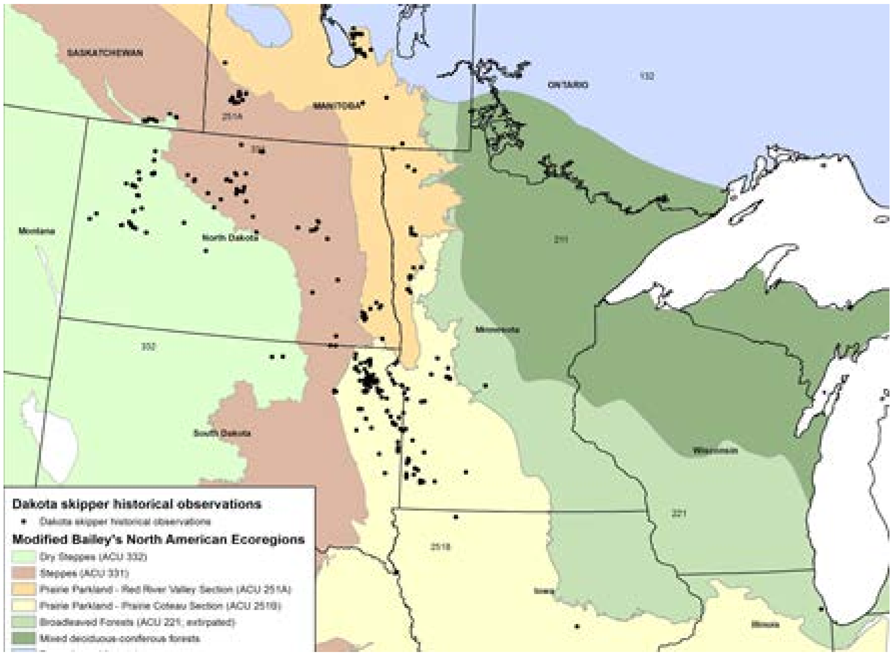


Figure 1.5. The Bailey’s North American Ecosystem Provinces (modified) covering the documented range of Dakota Skipper

Uncertainty

Our analyses rely on available data, expert judgments regarding the consequences of interacting influences, and our assessment of future state conditions. Because we do not fully understand the causal, interacting relationships and are unable to predict future state conditions with certainty, our analyses are necessarily predicated upon numerous assumptions, which could lead to over- and underestimates of viability. We identify the fundamental assumptions used and discuss the implications of these assumptions in Chapter 7.

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[1] The corresponding numbers relate to EcoRegion Codes that are embedded in the original dataset for Bailey’s Ecoregions of the United States and are used as a quick reference in tables and figures.

Chapter 2. Species Ecology

In this chapter, we briefly describe Dakota skipper taxonomy and discuss the species' life history characteristics at the individual, population, and species levels. This is not an exhaustive review of the species natural history; rather, it provides the ecological basis for the SSA analyses conducted in Chapters 3-7.

2.1 Species Description and Taxonomy

The Dakota skipper is in the insect class, Lepidoptera order, in the Hesperiidae family (subfamily Hesperiinae, grass skippers). Dakota skipper was first described in 1911 from collections taken at Volga, South Dakota, and Grinnell, Iowa (Skinner 1911 in Royer & Marrone 1992). The family Hesperiidae includes three other subfamilies and the genus Hesperia contains 18 species (Miller & Brown 1981; Ferris 1989 in Royer & Marrone 1992).

The Dakota skipper is a small to medium-sized butterfly with a wingspan of 2.4–3.2 centimeters (cm) [0.9–1.3 inches (in)] and hooked antennae (Royer and Marrone 1992, p. 3). Adult Dakota skippers have variable markings. The dorsal surface of adult male wings ranges in color from tawny-orange to brown and has a prominent mark on the forewing; the ventral surface is dusty yellow-orange (Royer and Marrone 1992, p. 3). The dorsal surface of adult females is darker brown with diffused tawny orange spots and a few diffused white spots restricted to the margin of the forewing (Fig. 2.1); the ventral surfaces are dusty gray-brown with a faint white spotband across the middle of the wing (Royer and Marrone 1992, p. 3). Adult Dakota skippers may be confused with the Ottoe skipper (*H. ottoe*), which is somewhat larger with proportionally longer wings (Royer and Marrone 1992, p. 3). Dakota skipper pupae are reddish-brown, and the larvae are light brown with a black collar and dark brown head (McCabe 1981, p. 181) with early instars being described as green with dark head and collar (Dana, *pers comm.*, 2018)(Figure 2.2).

2.2 Individual-level Ecology

Dakota skippers are univoltine (having a single flight per year), with an adult flight period that may occur from the middle of June through the end of July (McCabe 1979, p. 6; McCabe 1981, p. 180; Dana 1991, p. 1; Royer and Marrone 1992, p. 26; Skadsen 1997, p. 3; Swengel and Swengel 1999, p. 282). Actual flight periods vary somewhat across the range of the species and can also vary locally from year-to-year (e.g., Rigney 2013, p. 138), depending on temperature patterns (Bink and Bik 2009, Koda and Nakamura 2012). Females emerge slightly later than males (Dana 1991, p. 15, Rigney 2013, p. 138), and the observed sex ratio of Dakota skippers was roughly equal during peak flight periods (Dana 1991, p. 15; Swengel and Swengel 1999, pp. 274, 283).

The Dakota skipper flight period in a locality lasts two to four weeks, and mating occurs throughout this period (Braker 1985, p. 46; McCabe and Post 1977a, p. 38; McCabe and Post 1977b, p. 36; McCabe 1979, p. 6; McCabe 1981, p. 180; Dana 1991, p. 15; Swengel and Swengel 1999, p. 282; Rigney 2013, p. 138). Adult male Dakota skippers exhibit perching behavior (perch on tall plants to search for females), but occasionally appear to patrol in search of mating opportunities (Royer and Marrone 1992, p. 25).

Dakota skippers lay eggs on broadleaf plants (McCabe 1981, p. 180) and grasses (Dana 1991, p. 17), although larvae feed only on grasses. Potential lifetime fecundity is between 180 and 250 eggs per female Dakota skipper; realized fecundity depends upon longevity (Dana 1991, p. 26). Female Dakota skippers lay eggs daily in diminishing numbers as they age (Dana 1991, pp. 25–26). Dana (1991, p. 32) estimated the potential adult life span of Dakota skipper to be 3 weeks and the average life span (or residence on site before death or emigration) to be 3 to 10 days on one Minnesota prairie.

Dakota skippers overwinter as larvae and complete larval development in the spring. Dakota skipper eggs hatch after incubating for 7–20 days; therefore, hatching is likely completed before the end of July. The Minnesota Zoo demonstrated that under controlled conditions in the laboratory, Dakota skipper eggs hatched after 11 to 16 days, and the majority of the caterpillars hatched on the 13th and 14th days (Fig. 2.2., Runquist 2014, pers. comm.).

After hatching, Dakota skipper larvae (Fig. 2.2) crawl to the bases of grass plants where they form shelters of silk at the ground surface, fastened on an armature of plant tissue (Dana 1991, p. 16). Dakota skippers have six or seven larval stages (instars) and construct 2–3 successively larger shelters as they grow (Dana 1991, pp. 14–16). They overwinter (diapause) in ground-level or subsurface shelters during either the fourth or fifth instar (McCabe 1979, p. 6; McCabe 1981, pp. 180, 189; Dana 1991, p. 15; Royer and Marrone 1992, pp. 25–26). Final stage Dakota skipper larvae develop patches of secretory tissue on the ventral surface of two abdominal segments that produce a strongly hydrofugic flocculent white material. These "hydrofuge glands" aid in respiration in semi-aquatic environments and suggest a historical or present need of the species for protection from flooding (McCabe 1981, p. 181). Royer et al. (2008, p. 2) hypothesize that temperature and relative humidity at or near the soil surface may be important factors dictating larval survival, particularly since early stages live in a silken nest within a few centimeters (2–3) (0.8–1.2 in) of the soil surface during most of the summer (McCabe 1981, pp. 180–181, 189; Dana 1991, p. 16). In the spring, larvae resume feeding and undergo two additional molts before they pupate. During the last two instars, larvae shift from buried shelters to horizontal shelters at the soil surface (Dana 1991, p. 16).

When Dakota skipper larvae metamorphose into adults in late June or early July, habitats must provide nectar sources that are sufficient in quality and quantity to meet the butterflies’ water and nutritional requirements.

Nectar

Access to nectar during the flight period is a critical need for adult Dakota skippers. Females may realize lower fertility in areas with low nectar availability or may simply abandon such areas (Dana 1991, p. 53). Low nectar availability (low floristic quality) may be a result of invasion by grasses such as smooth brome and Kentucky bluegrass, which are both known to displace native forbs (and native grasses). Although Dakota skippers have been observed nectaring from nonnative forbs (i.e. white sweetclover, Melilotus alba; Rigney 2013a, p.4, 57), they have overwhelmingly been observed nectaring from native forbs. In addition to nutrition, the nectar of flowering forbs provides water for adult Dakota skippers, which is necessary to avoid desiccation during flight activity (Dana 1991, p. 47; Dana 2013, pers. comm.). “Regular access to nectar is clearly important” for adult Dakota skippers, likely as a source of water and secondarily as a source of carbohydrates to support survival and reproduction (Dana 1991, p.

47). Adult Dakota skippers nectar on flowers “regularly throughout the day” and do not obtain water from mud, pond margins, etc. as do other skippers (Dana 1991, pp. 21; 48).

Figure 2.1. Adult male – stigma on upper side of wing not visible in this photo (upper left); adult female (upper right).

Figure 2.2. Dakota skipper larva emerging from egg; later stage larva.

Nectar and water sources for adult Dakota skippers vary regionally and by habitat type (referred to as Type A’ and ‘Type B’ Dakota skipper habitat by Royer et al. 2008, p. 14-16 and described in further detail on Page 26, Dakota Skipper Habitat). ‘Type A’ habitat consists of low wet-mesic prairie with little topographic relief that occurs on near-shore glacial lake deposits that may be more prone to flooding and are dominated by bluestem grasses, with wood lily, bluebell bellflower, and mountain deathcamas almost always present (McCabe 1981, p. 190). ‘Type B’ habitat occurs primarily on rolling terrain over gravelly glacial moraine deposits and is dominated by big bluestem, little bluestem, and needle-and-thread or porcupine grasses.

When favored nectar species are unavailable, Dakota skippers may switch to less favored species that may produce less nectar or are accessible to a large number of other insects (Dana 1991, p. 48). In ‘Type B’ habitats in Minnesota, for example, Dakota skippers relied mostly on four plant species that have “concealed” nectar that is available only to species with a “slender trophic apparatus” (e.g., proboscis) that is 5 mm or longer (Dana 1991, p. 48; Table 1).

Plants that are important as nectar sources for Dakota skipper ‘Type A’ habitats appear to vary geographically, but blackeyed Susan (*Rudbeckia hirta L. var. pulcherrima*) is significant throughout the range of this habitat type (Habitat Types A and B are discussed in section 2.3 Population-level Ecology, under Dakota skipper Habitat). In Manitoba, most nectaring observed was on blackeyed Susan among 12 species documented as nectar sources (Rigney 2013, p. 59-62; Fig. 2.3). McCabe (1981, p. 187) also reported more sightings of nectaring on blackeyed Susan than on any other species in North Dakota ‘Type A’ habitats; he also reported the use of bluebell bellflower (*Campanula rotundifolia*) as a nectar source for the Dakota skipper in North Dakota (McCabe 1981, p. 187). Rigney (2013, p. 143) did not report nectaring on bluebell bellflower or prairie lily (*Lilium philadelphicum*) – two of the three primary indicators of ‘Type A’ habitat in North Dakota – and mountain deathcamas (*Zigadenus elegans*) comprised <1% of all nectaring observations. McCabe had earlier reported that “At no stage is the skipper dependent on camas…” and also reported that white prairie clover (*Dalea candida*) was “(A)vailable at most sites, but not used.” (McCabe 1981, p. 190), whereas it comprised 5% of nectaring visits recorded by Rigney (2013).

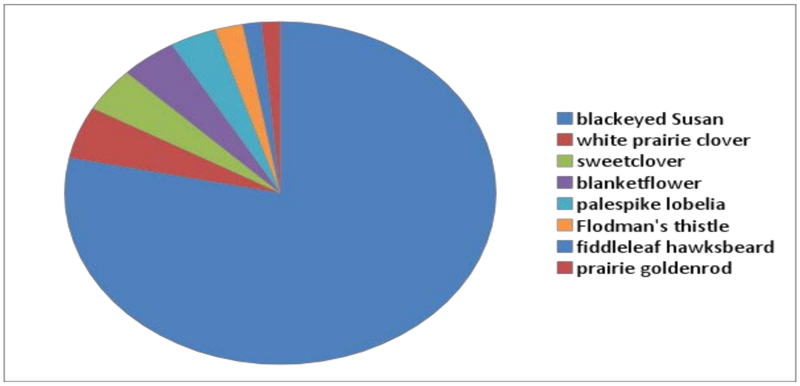


Figure 2.3. Plant species reported as nectar sources for Dakota skipper in ‘Type A’ habitats based on 147 nectaring observations made by Rigney (2013, p. 59-62) in Manitoba.

Alternatively, for the Dakota skipper in ‘Type B’ habitats, purple coneflower (*Echinacea angustifolia*) is especially important (McCabe 1981; Dana 1991; Swengel and Swengel 1999, pp. 280–281). Dana (1991, p. 21) reported the use of 25 nectar species in Minnesota with purple coneflower most frequented (Table 2.1); McCabe (1979, p. 42; McCabe 1981, p. 187) observed Dakota skippers using eight nectar plants, including purple coneflower. North of the range of the purple coneflower in Minnesota at Lake Bronson State Park, Dakota skippers used oval-leaf milkweed (*Asclepias ovalifolia*) and prairie milkvetch (*Astragalus adsurgens*) for nectar. In Minnesota, almost all nectaring occurred in dry-mesic habitat (Dana 1991, p. 50).

Table 2.1. Four species used most as nectar sources by Dakota skippers in Minnesota 'Type B' habitats (Dana 1991). Number of nectaring observations by Dana: V = very common (many hundreds, not enumerated); C = common (about 35 visits); F = frequent (11-25); 0 = occasional (1-10); R = rare (2-4).

Species	**Males**	**Females**
Purple coneflower (*Echinacea angustifolia*)	Very common	Very common
Prairie milkvetch (*Astragalus laxmannii* var. *robustior*)	Common	Frequent
Hoary vervain (*Verbena stricta*)	Occasional	Frequent
Purple locoweed (*Oxytropis lambertii* var. *lambertii*)	Frequent	Rare

The flight period of the adult female typically continues beyond that of males (Dana 2014, pers. comm.; Dana 1991, pp. 1,15; Rigney 2013, p. 138), therefore the two sexes can visit the same nectar plant species at different rates. For example, Dana (1991, p. 21) observed a greater number of males than females visiting purple locoweed; this plant is already past its flowering peak at the beginning of the male flight and nearly finished flowering by the peak female flight (Dana 2014, pers. comm.).

Habitat structure and composition

Dakota skippers use vegetation that rises above the grass canopy for reproduction as perches from which to spot and pursue potential mates. Females oviposit on plants "in the grass stratum" with little or no selectivity among plant species (Dana 1991, p. 14; 47). This lack of selectivity may be an adaptation to the ubiquity of the native grass species that function as larval food plants in high quality Dakota skipper habitat (see Larvae and Pupae, below). In Minnesota sites inhabited by Dakota skipper, Ottoe skipper (*H. ottoe*) larvae emerged from eggs laid on purple coneflower and dropped from the flowers into underlying grasses soon after hatching (Dana 1991, p. 77). Dakota skippers may behave similarly after hatching, although they may not oviposit frequently on purple coneflower (Dana 1991, p. 17).

Dakota skipper larvae feed on several native grass species; little bluestem (*Schizachyrium scoparium*) is a frequent food source of the larvae (Dana 1991, p. 17; Royer and Marrone 1992, p. 25) although they have been found on *Dichanthelium* spp., and other native grasses (Royer and Marrone 1992, p. 25). The bunchgrasses, little bluestem, prairie dropseed, and sideoats grama (*Bouteloua curtipendula*), provide Dakota skipper larvae with a dense cluster of erect blades in proximity to "an abundance" of edible leaf tissue (Dana 1991, p. 46). Large leaf blades, leaf hairs, and the distance from larval ground shelters to palatable leaf parts preclude the value of big bluestem and Indiangrass (*Sorghastrum nutans*) as larval food plants, particularly at younger larval stages (Dana 1991, p. 46). Similarly, invasive grass species smooth brome and Kentucky bluegrass are available when Dakota skipper larvae begin feeding, however, the morphology and growth habit of these grasses are likely determinants of their unsuitability to support Dakota skippers (Dana 1991, p. 46-47). In one captive larval host plant study, Dakota skippers that were only given smooth brome and Kentucky bluegrass resulted in reduced survivorship, reduced weight and delayed pupation (Runquist and Nordmeyer 2018, p.5). The strong correlation between occurrence of Dakota skippers and the dominance of native grasses in the habitat, indicates that population persistence requires native grasses for survival (R. Dana, Minnesota Department of Natural Resources, 2013, pers. comm.).

Table 2.2. The ecological requisites for survival and reproductive success of individuals

Life Stage	**Resource element**	**Resource function**	**Notes**
Adults	Native grass species, Native flowering forbs, water source	Feeding, Sheltering	
	Habitat structure: mid-height grasses; If present, trees or large shrub cover less than 5% and 25% of area in dry and wet mesic prairies, respectively	Reproduction	Mid-height grasses provide perches for males, which need unobstructed flight path from perches to chase rivals, search for mates.
Egg	Native grasses, broadleaf plants, dry-mesic habitat	Sheltering	Habitat must not be subject to intense herbivory or fire when eggs are present.
Larvae and Pupa	Native grass species; soil surface (0-2cm) microclimate	Feeding, sheltering	Little bluestem (*S. scoparium*) is frequent larval food source. Temperature and relative humidity near soil surface may be important for larval survival.

2.3 Population level Ecology

As explained in Chapter 1, Methods, Dakota skipper population structure most likely resembled a true metapopulation structure historically. In true metapopulations we would assume that all subpopulations are subject to extirpation and that the probability of extirpation is inherently identical but independent (asynchronous) among subpopulations. Recolonization is slow and occurs at a rate that increases when there are more subpopulations. Persistence of the metapopulation depends on the fate of the individual subpopulations, but also on the influence of barriers to dispersal (USFWS 2003, p. E-53).

For this assessment, we grouped the remaining local populations of the Dakota skipper into metapopulations that are groups of subpopulations that inhabit discrete remnants of native prairie near enough to one another such that dispersal is reasonably likely to occur. Due to the widespread extirpation of the species, however, many of the remaining populations do not function as metapopulations - they cannot receive immigrants and the prairie remnant would not be recolonized by the species in the event of its local extirpation. Thus, they are metapopulations in name only.

The number of individuals comprising a metapopulation (population size, N) influences population viability through the processes of demographic, genetic, and environmental stochasticity. Metapopulation persistence requires robust demography and genetics, as well as, sufficient habitat to support a healthy demography. Below, we describe the demographic, genetic, and habitat requisites for a healthy--successfully recruiting—metapopulation; these population level needs are summarized in Table 2.3.

Demographic & Genetic Considerations

Small and isolated populations have low levels of genetic diversity, which reduces their capacity to respond to environmental change and can reduce population fitness via reductions in longevity, fecundity, offspring viability, and dispersal (Darvill *et al.* 2006, p. 608; Mattila et al. 2012). A positive relationship between genetic diversity and dispersal is mediated by proximate factors like flight metabolic rate, which can be diminished in small populations with low genetic diversity (Mattila et al. 2012, E2502; Hanski 2011, p. 14401-14402; Niitepõld et al. 2009, p. 2230; Vandewoestijne et al. 2008, p. 8). Low genetic diversity can also reduce longevity of butterflies and, thus, reproductive output (Vandewoestijne et al. 2008). In addition, preservation of allelic diversity - the variety of alternate forms of genes - influences a population's ability to persist in the face of environmental change. High allelic diversity increases the likelihood that individuals will be adapted (i.e., possess genotypes that facilitate high survival) for varying environmental conditions. The interactions between genotype and temperature on flight metabolic rate and dispersal rate in Glanville fritillary butterflies (*Melitaea cinxia*), for example, strongly suggest that heterozygotes at a specific gene can reach higher levels of activity than homozygotes at low ambient and body temperatures but perform poorly at high temperatures (Niitepõld et al. 2009, p. 2230). Having individuals with both gene combinations will ensure the population can persist through differing environmental conditions.

Genetic variation can be loss through genetic drift, which is driven by low effective population sizes (Ne, Zayed 2009, p. 246). Thus, preserving the genetic diversity of the Dakota skipper requires maintaining large populations and connectivity among the populations. In the absence of a population viability analysis (PVA) to support population targets, rules of thumb based on meta-analyses of published PVAs have been proposed (Rosenfeld 2014, p. 287). Frankham et al. (2014) most recently proposed that minimum viable population sizes of 100/1000 may be appropriate targets to minimize the likelihood of inbreeding depression and to ensure long term adaptive capacity, respectively. The Dakota skipper is among the threatened species for which data are not available to identify credible minimum viable population sizes (Rosenfeld 2014, p. 287). Population sizes reported for Dakota skipper vary among sites and temporally within sites. Royer and Marrone (1992) reported densities of 40 individuals/ha in North Dakota. Dana (1991, p. 1) reported a 25 individuals/ha during peak abundance at a site in Minnesota; based on mark-recapture-recovery work, he estimated that the total seasonal [meta]population was 2,000-3,000 adults. At a 25-ha prairie in Manitoba, the average density was 23.5 individuals/ha (COSEWIC 2003, p.19); extending this estimate across the sites gives a [meta]population size of 500 individuals.

The health of a population is also determined by its long-term population growth rate (lambda, λ). A λ of at least 1.0 is needed for a population to persist; species that are sensitive to environmental conditions tend to fluctuate and thus require strong growth rate potential to recover from years when survival or reproduction are low. The long-term λ needed to sustain a Dakota skipper population over time is unknown. Butterflies are sensitive to environmental conditions, however, and experience swings in population numbers from year-to-year that vary among species according to life-history and other factors (Mason et al. 2017). Thus, they must have growth potential that is strong enough to recover from years when environmental or human-caused factors result in low survival or reproduction. Population monitoring at a few sites suggests that inter-annual fluctuations in Dakota skipper abundance may be low during some periods (McCabe 1981, Dana 1991, 1997); Dana (1997, p. 14), however, cites evidence that significant year-to-year fluctuations in population size do sometimes occur.

Population health is also affected by dispersal. Although evidence for a positive relationship between adult density and dispersal is not consistent among butterfly species (Konvicka et al. 2011, p. 98; Nowicki and Vrabec 2011, p.663), there is growing evidence that dispersal is positively related to genetic diversity and that genetic diversity is higher in large populations (Vandewoestijne et al. 2008, p. 5). Dispersal is necessary for the Dakota skipper to recolonize prairie remnants from which it has been extirpated and also facilitates gene flow, reducing the potential for genetic drift and inbreeding depression. Genetic drift is more likely to occur when populations are small and isolated.

Healthy metapopulations rely on discrete high quality habitat patches that are separated by less than one kilometer and are embedded in a landscape matrix with few or only minor barriers to dispersal. We assume that all three factors - short distances separating patches; high quality habitat; and, few or no dispersal barriers - are essential to ensure healthy metapopulation function, but we are uncertain of their relative importance. In a study of another butterfly species with “rather low dispersal ability” distance was most important determinant of dispersal; habitat quality in recipient patches was second in importance, whereas matrix composition was of less importance (Kalarus and Nowicki 2015, p.9). The Dakota skipper may not typically move greater than 1 kilometer (km) (0.6 miles (mi)) between habitat patches separated by structurally similar habitats, such as crop fields, grass-dominated fields or pasture. Dana (1991, pp. 30-40) found the average distances between recaptures of marked Dakota skippers less than 300 meters (m) (984 feet (ft)) over 3–7 days and observed movements of less than 200 m (656 ft) between patches of unsuitable habitat. Similarly, Dana (1997, p. 5) observed less movement across a small valley dominated by exotic grasses compared with movements in adjacent widespread prairie habitat. He also indicated that roads and crop fields may be impediments for movement (Dana 1997, p. 5). Skadsen (1999, p. 2) reported possible movement of Dakota skippers in 1998 between two areas separated by at least 800 m (2625 ft); the area between the two patches consisted of native vegetation of varying quality, interspersed by a few asphalt and gravel roads (Skadsen 2001, pers. comm.). Habitat quality in the recolonized patch may have played an important role in the recolonization - the year the movement occurred the site had an unusually heavy growth of purple coneflower; he had not found Dakota skippers at this site in three previous years when coneflower production was sparse.

Lastly, population health is influenced by the timing of events. Like many Lepidoptera, Dakota skipper phenology is somewhat annually variable (Dana 1991, p. 46). Peak flight times occur within a span of about 10 days in early July each year. This period is particularly important in maintaining genetic variability in Dakota skipper populations because the largest number of broods are represented in mating adults at this time (Britten and Glasford 2002, p374). Thus, disruptive activities during the peak flight period can substantially reduce the genetic as well as the demographic health of a population.

Habitat Considerations

The capacity for Dakota skipper populations to grow is limited by the quantity and quality of the habitat and by connectivity among habitat patches. The minimum extent of habitat that is sufficient to support a healthy local population is unknown, but discrete populations have been recorded in prairie remnant patches as small as one acre. Populations in patches this small likely rely heavily on the existence of populations in nearby patches to ensure their long-term persistence.

Dakota skipper habitat consists of two general types. The first type is a low wet-mesic prairie with little topographic relief that occurs on near-shore glacial lake deposits (Figure 2.4); Royer et al. (2008, p. 14-16) refer to this as ‘Type A’ Dakota skipper habitat. This habitat type occurs primarily in North Dakota and Central and Western Manitoba, but it may also comprise a small amount of the species’ habitat in northeastern South Dakota (Skadsen 1997, p. 4) and in the Interlake Region of central Manitoba (Westwood, *pers comm., 2018*). ‘Type A’ habitat may be flooded in some years, but has “sufficient relief to provide segments of non-inundated habitat during the spring larval growth period within any single season” (Royer et al. 2008, p. 15; Royer et al. 2014, p. v). ‘Type A’ Dakota skipper habitat is dominated by bluestem grasses, with three other plant species almost always present and blooming during Dakota skipper's flight period: Wood lily, bluebell bellflower, and mountain deathcamas (McCabe 1981, p. 190).

The second Dakota skipper habitat type, referred to as ‘Type B’ by Royer et al. (2008, p. 14), occurs primarily on rolling terrain over gravelly glacial moraine deposits and is dominated by big bluestem, little bluestem, and needle or porcupine grasses (*Hesperostipa* spp.) (Figure 2.5). In Minnesota, many historically occupied sites (and one currently occupied) are shoreline complexes created by glacial Lake Agassiz and consist of low, variably broad ridges or scarps of sandy-gravelly soil supporting mesic to dry prairie (predominantly dry-mesic) with no flooding susceptibility. Some ‘Type B’ habitats occur in several valleys in the western population in Manitoba where sites are mostly type A habitat. Dominant grasses in addition to those listed in ‘Type B’ habitat include side-oats grama, prairie dropseed and several *Dichanthelium* species. Dakota skippers do not extend beyond these habitats except perhaps to disperse to nearby patches, but their capacity to disperse is limited (see Dispersal, above). As in ‘Type A’ habitats, bluebell bellflower and prairie lily are present, but ‘Type B’ habitats also typically support extensive stands of purple coneflower, upright prairie coneflower (*Ratibida columnifera*), and common gaillardia (blanketflower, *Gaillardia aristata,* Royer et al. 2014, p. 1-2).

Figure 2.4. 'Type A' Dakota skipper habitat in North Dakota (left) and Manitoba (right) (Royer et al. 2014, Westwood pers comm. 2018).

Figure 2.5. 'Type B' Dakota skipper habitats in Minnesota (left) and South Dakota (right). USFWS photos.

Two key factors, soils unsuitable for agriculture and steep topography, have allowed remnant native-prairie habitats inhabited by Dakota skippers to persist (Royer and Marrone 1992, p. 22). McCabe (1979, pp. 17-18; 1981, p. 192) and Royer et al. (2008, p. 16) have linked the historical distribution of Dakota skippers to surface geological features and soils that are glacial in origin and, possibly, regional precipitation-evaporation ratios.

Periodic disturbance is required to maintain the suitability of a habitat patch. Without periodic disturbance habitat becomes unsuitable for Dakota skippers due to expansion of woody plant species (secondary succession), litter accumulation, reduced densities of adult nectar and larval food plants, or invasion by nonnative plant species (e.g., smooth brome) (McCabe 1981, p. 191; Dana 1983, p. 33; Dana 1997, p. 5; Higgins et al. 2000, p. 21; Skadsen 2003, p. 52). Historically, natural processes such as drought, flooding, fire, and herbivory maintained a shifting matrix of suitable habitat. Due to the disruption and loss of these natural disturbance processes, anthropogenic induced disturbances--namely, haying, grazing, and prescribed fire--have been essential in maintaining native prairie and the essential features of the Dakota skipper’s grassland habitats. However, given the short dispersal range for the species, the frequency and intensity of these management practices must not cause local extirpation.

- Fire

Dakota skipper are not immune to fire. Panzer (2002, p. 1306) identified life-history traits of duff-dwelling insects, like the Dakota skipper, that were good predictors of a negative response to fire: (1) upland inhabitance (dry uplands burn more thoroughly than wetter habitats); (2) nonvagility (poor dispersal ability that leads to low recolonization rates); and (3) univoltine (single annual flight periods that lead to slower recovery rates). The Dakota skipper meets all three criteria. When a species would meet a fourth criterion – isolation of populations into habitat fragments – Panzer would characterize it as hypersensitive to fire (Panzer 2002, p. 1306). However, Panzer also found that more than half of fire negative species recovered in one year or less post-fire (2002, p.1305). He and others posit that few if any insect species are threatened by careful use of cool-season prescribed fires (Panzer and Schwartz 2000, p. 365, Black et al. 2011, p.11).

Due to the depletion and fragmentation of Dakota skipper habitat, populations may now be largely isolated and must retain the capacity to recover from the effects of fire without relying on immigration. Dakota skipper populations existed historically in a vast grassland ecosystem and within its range its occurrence likely shifted locally in response to fires. Due to the great extent of tallgrass prairie in the past, fire and other intense disturbances (e.g., locally intensive bison, *Bison bison*, grazing) likely affected only small proportions of Dakota skipper habitat in most years; allowing it to recolonize burned areas during subsequent flight periods (Swengel 1998, p. 83). Today, the depletion and fragmentation of Dakota skipper habitat compounded by a changing climate has resulted in novel ecosystems not well-known or understood by land managers and making fire (and other prairie management actions) even more challenging. We discuss these challenges in more detail in Chapter 5. Ideally, sites should be divided into four or more units and fire rotated among units in early spring to reduce mortality and allow for recolonization from unburned areas (Cochrane and Delphey, 2002, p.37, Dana 1991, p.54-55, Moffat and McPhillips, 1993 p.5).

- Grazing

Bison grazed at least some Dakota skipper habitats historically (McCabe 1981, p. 190; Bragg 1995, p. 68; Schlicht and Orwig 1998, pp. 4, 8; Trager et al. 2004, pp. 237–238), but cattle (*Bos taurus*) are now the principal grazing ungulate in the species’ range. Bison and cattle both feed primarily on grass but have some dissimilar effects on prairie habitats (Damhoureyeh and Hartnett 1997, pp. 1721–1725; Matlack et al. 2001, pp. 366–367). Bison consume proportionally more grass and grass-like plants than cattle, whereas cattle consume more browse (woody vegetation) and forbs (flowering herbaceous plants) (Damhoureyeh and Hartnett 1997, p. 1719, Knapp et al. 1999, p.41). Grasslands grazed by bison may also have greater plant species richness and spatial heterogeneity than those grazed by cattle (Towne et al. 2005, pp. 1553–1555). Both species remove forage for larvae (palatable grass tissue) and adults (nectar-bearing plant parts) and change vegetation structure and they may also trample larvae and alter larval microhabitats. The difference today is that cattle (and bison) are confined and are often grazed season-long (May through October) regardless of the capacity of the site to sustain this grazing pressure, especially if it is continued year after year.

As with fire, proximity of nearby populations or contiguous habitat may alleviate some of the negative impacts of grazing. Royer and Marrone (1992b, p. 29; 1992a, p. 18) stated that heavy grazing was a threat to Dakota skippers and Poweshiek skipperlings (*Oarisma poweshiek*), but that occasional light grazing is not a long-term threat in some habitats as long as there are areas of contiguous habitat that remain ungrazed.

Grazing, regardless of rate, should be used in a manner that improves or maintains native prairie for Dakota skippers for the long term while minimizing adverse impacts. Land managers should have knowledge of the distribution of both larval and adult habitat when planning grazing activities. Sites should be divided if possible and rotational grazing used in a manner that at least some portion of a site is rested each year and the timing of grazing is varied (USFWS 2016, p.6). Skadsen (2003, p. 53) recommends stubble heights do not go below 20 cm (8”) in tallgrass prairie.

➢ Haying

Haying (grass mowing and removal of clippings) is used for maintenance of grass ecosystems, forage for livestock, and weed control. As with other management there are both pros and cons with this treatment. Some of the negative effects of haying are creating uniform plant height (reducing structural diversity), removing nectar sources, and direct mortality of eggs and larvae. However, some experts believe haying can be the best method to maintain prairie habitat and Dakota skipper populations (Swengel et al. 2010, Moffat and McPhillips 1993, p. 9, McCabe 1981, p. 190, Cochrane and Delphey 2002, p. 38). Haying is not always feasible especially in Type “B” habitats with hilly and rocky landscapes. As with other management, haying should be used judicially, preferably in late summer or fall, after the flight of Dakota skipper (McCabe 1981, Skadsen 2006). Dividing a unit and rotating mowed areas over years may further ensure the persistence of Dakota skippers (Moffat and McPhillips 1993, Dana 1991, Cochrane and Delphey 2002, p.38).

In summary, population health—ability to successfully recruit over time—requires robust demography (large N and strong λ) and genetics (large effective N and gene flow), as well as, sufficient habitat (well connected, heterogeneous prairie habitats) to support a healthy demography (Table 2.3). Habitat must be ‘disturbed’ to remain suitable, but as Dakota skipper is susceptible to habitat changes and is rarely found in prairie habitats that have been altered (McCabe 1981, p. 191), disturbance processes—in terms of the frequency, intensity, and timing--must be compatible with the species’ biology.

Table 2.3. Population level requisites to support a healthy Dakota skipper population

Parameter	Requirements
Population size, N	Sufficiently large N to withstand unfavorable years and to avoid deleterious effects from genetic drift and inbreeding depression.
Population growth rate, λ	Long-term lambda will need to sufficiently exceed 1 to recover from adverse environmental conditions.
Habitat quality & quantity	Large patches (population-specific, but generally 2000-3000 ac) of tall- and mixed-grass prairie with high plant species diversity in landscapes that retain high habitat heterogeneity
Disturbance dynamics (management practices)	Suitable intensity, frequency, and timing of disturbance
Connectivity	Suitable landscape matrix to allow movement between habitat patches, i.e., habitat patches <1000 m apart, on average and permeable landcover between patches

2.4 Species-level Ecology

The ecological requisites at the species level include having sufficient number, health, and distribution of populations to ensure it can withstand annual variation in its environment (resiliency), catastrophes (redundancy), and novel biological and physical in its environment (representation).

Resiliency

Resiliency is the ability to sustain populations in the face of environmental variation and transient perturbations. Dakota skipper resiliency is a function of the number of healthy populations and the distribution of these populations across heterogeneous conditions. A healthy population is defined above under “Population-level Ecology.” Maintaining populations across its north-south latitudes and across a diversity of environmental conditions help guard against concurrent losses of populations by inducing asynchronous fluctuations among populations. Given the Dakota skipper phenology, and thus exposure to region-wide “unfavorable” year varies by latitude, maintaining populations in the both the northern and southern portions of the range will foster population asynchrony (R. Dana, pers. comm. 2018). The environmental correlates most likely to influence Dakota skipper population dynamics include spring temperatures (i.e., cool springs), summer temperatures and precipitation (e.g., hot, dry summers; cool, wet springs), and flooding (in portions of North Dakota). The magnitude of influence these conditions pose depends upon habitat and landscape characteristics (e.g., aspect, topography, soils, etc.). Generally speaking, with a greater degree of spatial heterogeneity there will be less synchrony among Dakota skipper populations, thereby affording the species’ greater resiliency to environmental disturbance. Additionally, resiliency also requires connectivity among populations for gene flow and demographic rescue. Connectivity between subpopulations allows gene flow, and thus increases genetic health of a population.

Redundancy

Species-level redundancy reflects the ability of a species to withstand catastrophes (i.e., extraordinary events that would be expected to cause population extirpation), and is best achieved by having multiple, widely distributed populations of Dakota skippers relative to the spatial occurrence of catastrophic events. As further explained in Chapters 1 and 5, we identified drought as a plausible catastrophic factor. Although a species' ability to withstand catastrophes can be influenced by its health (i.e., a demographically robust population is more likely to withstand drought conditions), survival is most strongly influenced by exposure to such events. Exposure is a function of both the number of populations (the more populations, the less likely all will be exposed contemporaneously and to the same intensity) and the distribution of populations (the more widely distributed, the less likely all will be exposed). Thus, generally speaking, the greater the number of populations and the more widely distributed, the more redundancy Dakota skipper possesses.

Representation

Species-level representation reflects the ability of the species to adapt to novel changes in its environment. For adaptation to occur, there must be variation upon which to act (Lankau et al. 2011, p. 320) and functional evolutionary drivers. By maintaining the sources of diversity across the species' range, as well as the processes that drive evolution (particularly gene flow and natural selection), the responsiveness and adaptability of the Dakota skipper over time are preserved.

Diversity

Britten and Glasford (2002) conducted a rangewide survey of Dakota skipper populations to assess the levels of genetic variability and geographic scale of its population structure. They found small genetic divergence (genetic distance) among seven sites in Minnesota and South Dakota, which indicates that populations there were historically connected. This supports the presumption that Dakota skipper formerly had a relatively continuous distribution. They also found some genetic differentiation between the Manitoba populations and Minnesota and South Dakota populations (Britten and Glasford 2002, pp. 367, 372); but populations in additional intervening locations need to be sampled to confirm this hypothesis (Runquist 2012b, pers. comm.).

In addition to neutral genetic (insensitive to selection) diversity, it is important to preserve sources of the adaptive (sensitive to selection) diversity. Identifying the such sources requires long-term, controlled studies, and thus, rarely conducted. Instead, we rely on surrogate information. Upon reviewing the literature, we identified four reliable proxies for identifying sources of Dakota skipper adaptive diversity. These included three climatic variables, length of growing season, daily maximum temperature, and precipitation, and one biological factor, larval food plant species composition and diversity. Below we summarize for each factor why it is likely to reflect underlying genetic or phenotypic differences that will affect the ability of the Dakota skipper to adapt to changes in its environment.

- **Length of growing season/length of winter –** Butterflies that enter diapause before completing larval development, like the Dakota skipper, adapt to geographic differences in the length of the growing season and the duration of winter by adjusting how diapause is broken in spring. In the Dakota skipper, the larval period comprises about 90% of its annual life cycle. The timing of its entry into diapause in the fall and when diapause is broken in the spring may have significant adaptive importance across its range. The scientific literature contains evidence for butterfly adaptations to variations in the length and severity of winter. Variation in diapause duration of *Pieris napi* across a latitudinal gradient, for example, suggests that it is adapted locally to the length of winter and that there may be "evolutionary costs associated with early diapause termination" (Posledovich et al. 2015). The Dakota skipper requires fewer degree days to break diapause in Manitoba than appears to be required in the southern part of the species' range, a possible adaptation to shorter growing seasons in the north (Dearborn and Westwood 2014).

- **Average daily maximum temperature –** As has been demonstrated for other species, the Dakota skipper may have developed thermoregulatory strategies for one or more life stages in response to the maximal summer heat levels experienced throughout its range. These adaptations may vary among portions of the species' range in response to variations in heat maxima. Kleckova and Klecka (2015) maintained that the primary "selective agents driving the evolution of thermoregulatory strategies are temperature extremes, rather than long-term means." They also cite "mounting evidence that tolerance to heat does not evolve as easily as tolerance to cold" and that "the effect of temperature may differ across developmental stages." Although the authors state "that maximal temperatures seem to be more limiting than minimal temperatures in terrestrial ectotherms", the Dakota skipper may have adapted to deal with both the hot and relatively cool conditions that they may encounter across its range. Adaptation of Canadian tiger swallowtail (*Papilio canadensis*) to short cool summers in parts of its range, for example, has been accomplished in part through a general elevation of metabolic activity at all temperatures (Ayres and Scriber 1994).

- **Precipitation (drought frequency and intensity) –** One or more life stages of the Dakota skipper may have evolved to the levels of drought experienced in its geographic area. As summarized by Danks (2007, p. 15), insect adaptations to drought "can be selected relatively rapidly" and include those that serve to limit water loss, acquire water, or tolerate water loss.

- **Larval food plant species composition –** Insect larvae adapt to traits of host plants that vary among plant species, including changes in body part size. These adaptations include both phenotypic plasticity and heritable physiological traits (Ohata et al. 2011). Adaptations may include acquisition of specific detoxification enzymes (Karban and Agrawal 2002) and anatomical adaptations, such as increased gut size, which may increase ability to use novel food plants (Ohata et al. 2011:65). The Dakota skipper is a grass-feeder and the relative abundances of native grasses in its habitats vary throughout its range. Although specific adaptations to different larval food plants have not been described for Dakota skipper, it is reasonable to assume that variation in grass species composition of the species' habitats across its range has resulted in important adaptations.

Evolutionary Processes: Gene Flow, Genetic Drift, and Natural Selection

Maintaining the adaptive capacity of a species also requires preserving the processes-- natural selection, gene flow, and genetic drift (Zackay 2007, p. 1; Crandall et al. 2000, p. 291)--that allow for evolution to occur (Crandall et al. 2000, p. 290; Sgro et al. 2011, p. 327). Natural selection is the process by which heritable traits can become more (selected for) or less (not selected for) common in a population by favoring those traits that enhance survival (Hendry et al. 2011, p. 169). To preserve natural selection as a functional evolutionary process, it is necessary to maintain populations across the breadth of biological and ecological conditions (i.e., maintaining populations across historical latitudinal, longitudinal, and elevational gradients, as well as climatic gradients) to which the species may continue to adapt.

Gene flow influences genetic diversity by introducing new alleles into a population, and hence, increasing the gene pool size. As explained above, historically, gene flow likely served as a strong evolutionary force. Ensuring genetic connections among populations as close to historical patterns as possible helps preserve the effectiveness of gene flow as an evolutionary process (Crandall et al. 2000, p. 293). Genetic drift influences the frequency of alleles in a population via random, stochastic events, and can lead to reduced variation. Genetic drift is most influential in isolated populations and those with small effective population sizes (Zackay 2007, p. 246). For these reasons, Britten and Glasford (2002, p. 373) suggest that Dakota skipper populations be managed at high (genetically effective) population sizes and genetic connections preserved to ameliorate the erosive effects of genetic drift.

Adaptive Capacity Units

Given the above, and as explained in Chapter 1 under *Methods*, we selected the ecological classification developed for the United States by Robert Bailey (Bailey 1983; Bailey 1995) and as adapted for North America (Bailey 1998) to delineate areas of unique adaptive capacity. Specifically, we chose Province scale to delineate Dakota skipper diversity and refer to the Provinces as Adaptive Capacity Units (ACU). See Chapter 1 for our rationale for choosing the Bailey’s North Ecoregion Provinces and refer to Figure 1.5 for a visual depiction of the Dakota skipper ACUs.

Given the above, the species level requisites for Dakota skipper include having multiple healthy populations occupying heterogeneous conditions in the southern and northern portions of its and within each of the ACUs (Table 2.3 and 2.4).

Table 2.4. Summary of species-level ecological requisites for Dakota skipper

3Rs	**Species-level Requisites**	**Details**
Resiliency	Healthy populations distributed across environmental and habitat heterogeneous conditions	Environmental heterogeneity is having populations occupying areas with temperature and precipitation gradients. Habitat heterogeneity is having populations occupying wet and dry habitats, as well as, both north and south facing slopes.
Redundancy	Healthy populations distributed across geographical areas with low risks to catastrophic droughts and widespread pest control events	The intensity and duration of drought causing catastrophic losses is unknown, but drought similar intensity to the Dust Bowl of the 1930s is likely to cause population collapse.
Representation	Having healthy populations representing the breadth of adaptive diversity and maintaining evolutionary processes	Adaptive diversity is the variation in genetic and phenotypic traits that control the ability of the species to adapt to novel changes. To ensure the breadth of adaptive diversity is preserved, we should maintain populations in the ACUs and connectivity among populations to ensure gene flow and minimize genetic drift.

Chapter 3. Analysis of the Historical Condition

For the purposes of our analyses, the historical condition is the reference condition providing the context for the current and future conditions. That is, historical condition is the baseline from which the current and future degrees of resiliency, representation, and redundancy are measured.

Historically, the species occurred throughout the vast grasslands of the north-central United States and south-central Canada, extending from Illinois to Saskatchewan (Figure 3.1, Table 3.1). There were few records for the species prior to 1960s, so our ability to describe the species' historical distribution is limited. The southernmost and easternmost records in Iowa and Illinois suggest that the species occurred in at least some portions of the prairie that once covered much of these two states, but whose almost complete destruction began in the 1800s. Based on all known records, at least 145 metapopulations and approximately 303 subpopulations can be identified (Table 3.2). It is likely, however, that these delineated populations are artifacts that have resulted from the heavy destruction and fragmentation of the species' habitat. It is unclear to what degree distinct populations existed historically and what areas may have contained large panmictic breeding populations. The small genetic differences among seven Dakota skipper populations in the southern portion of the species' range that are now disjunct, for example, suggest that they were formerly connected prior to European settlement (Britten and Glasford 2002, pp. 371–372).

Dakota skippers have been documented in 5 adaptive capacity units (Table 3.2), but the distribution is not symmetrical (Figure 3.1). Nearly half of Dakota skipper records are from the Prairie Parkland - Prairie Coteau (ACU 251B), mostly in Minnesota and South Dakota with fewer and more dispersed records located in Manitoba, North Dakota and Iowa. Prairie Parkland - Red River Valley (ACU 251A). The Steppes Ecoregion Province (ACU 331) and Dry Steppes Ecoregion Province (ACU 332) are similar to ACU 251A in terms of the number of occurrences. In ACU 331, most of the records are from North Dakota and Manitoba, with fewer and more dispersed records from South Dakota. In ACU 332, most of the records are from northwest North Dakota and a small cluster in Saskatchewan with a couple isolated occurrences in South Dakota. The Broadleaf Forest- Continental Ecoregion Province (ACU 221) had far fewer records, with only 2 records.

To assess changes in spatial heterogeneity, we summarized the distribution of recorded populations of the Dakota skipper at section/ecoregion scale. Populations were distributed among 12 distinct sections (Table 3.3). The numbers of populations shown is likely a poor indicator of the species' relative abundance among the Sections and Ecoregions because the destruction of the prairie was early and nearly complete in certain sections, such as the Central Dissected Till Plains and the Minnesota & Iowa Morainal and Oak Savannah.

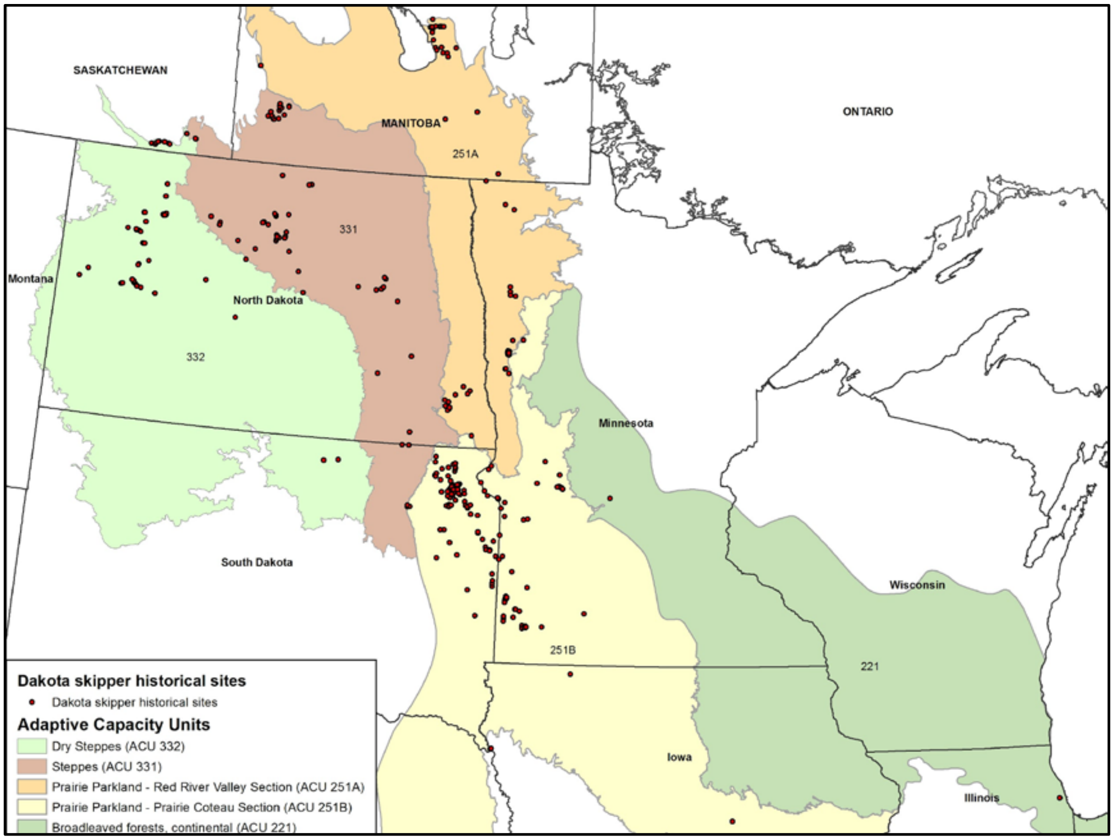
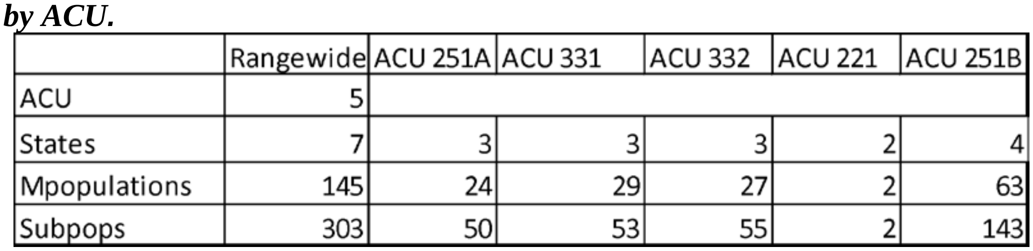


Figure 3.1. The historical distribution of Dakota skipper. Color zones represent the 5 Adaptive Capacity Units [from West to East]: Dry Steppes Ecoregion Province (ACU 332), Steppes Ecoregion Province (ACU 331), Prairie Parkland - Red River Valley (ACU 251A)., Prairie Parkland - Prairie Coteau (ACU 251B), and Broadleaf Forest- Continental Ecoregion Province (ACU 221)

Table 3.1. Number of metapopulations and subpopulations by State

State/ Province	# of Metapopulations	# of Subpopulations
IL	1	1
IA	3	3
MN	36	36
ND	45	70
SD	38	90
MB	19	12
SK	5	91

Table 3.2. The known number of ACUs and States/Provinces occupied by Dakota skipper historically; the number of, metapopulations and subpopulations rangewide and by ACU.



	Rangewide	ACU 251A	ACU 331	ACU 332	ACU 221	ACU 251B
ACU	5					
States	7	3	3	3	2	4
Mpopulations	145	24	29	27	2	63
Subpops	303	50	53	55	2	143

Table 3.3. The distribution of recorded metapopulations and subpopulations within Bailey's Sections (U.S.) and Ecoregions (Canada - A National Ecological Framework for Canada, http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html).

Section/Ecoregion	ACU	# of Meta-populations	# of Sub-populations
Central Dissected Till Plains	251B	2	2
Interlake Plain (Canada)	251A	1	1
Lake Manitoba Plain (Canada)	251A	11	20
North-Central Glaciated Plains	251B	68	129
Red River Valley	251A	18	25
Aspen Parkland (Canada)	331	9	16
Moist Mixed Grassland (Canada)	332	5	11
Northeastern Glaciated Plains	331	28	46
Western Glaciated Plains	331	1	3
Northern Glaciated Plains	332	11	28
Northwestern Great Plains Section	332	7	14
Minnesota & Iowa Morainal and Oak Savannah	221	2	2

Chapter 4. Analysis of Current Conditions

In this chapter, we review the current condition—the number, health, and distribution--of Dakota skipper populations. See Chapter 1 for a description of our methodology.

Rangewide Condition

The current distribution of Dakota skipper is depicted in Figure 4.1. In early 2000s, an increase in the extirpation of Dakota skipper populations became evident, with drastic declines observed since 2010. As of 2017, 75 metapopulations consisting of 157 subpopulations persist across 5 states (Table 4.1). The species is believed extirpated from Illinois and Iowa; the last known occurrence of Dakota skipper in Illinois was 1911 and 2000 in Iowa.

The health of many of the remaining metapopulations appears low (Figure 4.2), with 42 (56%) of the metapopulations having a predicted probability of persistence of less than 0.50 (Figure 4.3). The health of these populations may be overstated. Our model assumes functional connectivity between subpopulations. We know, however, that many of the metapopulations are highly fragmented (see Chapter 5), and thus, dispersal between subpopulations is not certain as our model assumes.

Looking at subpopulation health can give further insights into metapopulation health. For the majority of the subpopulations, health is very low (Figure 4.4). Only five subpopulations have more than 70% chance of surviving over the next 10 years and none have a greater than 80% chance; the vast majority (78%) have less than 50% chance and 19% of the subpopulations have a 1 in 5 chance of surviving (Figure 4.4).

Along with the loss of populations, the degree of spatial heterogeneity declined as well. Populations persist in 9 of 12 historically occupied sections/ecoregions (Table 4.2). The loss of the species from the Central Dissected Till Plains reflects the extirpation of the species sometime after 1911 from a large part of Iowa that was formerly covered by tallgrass prairie. The loss of the species from the Interlake Plain in Canada occurred much more recently - it was recorded as recently as 2000 in the Tallgrass Prairie Preserve in Manitoba. Few populations remain in the Red River Valley Section. Populations in the North-Central Glaciated Plains Section - primarily in northeastern South Dakota - and in the Lake Manitoba Plain (Canada) Ecoregion are separated by approximately 500 km and inhabit markedly different habitat types - Type A habitats on in the Lake Manitoba Plain Ecoregion and Type B habitats, predominantly, in the North-Central Glaciated Plains Section.

Adaptive Capacity Unit Condition

The number of populations has declined in all ACUs, with extirpation of ACU 221 (Table 4.1). Within ACU 251B, 25 metapopulations consisting of 63 subpopulations persist today, which represents a 60% and 67% decline in the number of metapopulations and subpopulations, respectively (Figures 4.6 and 4.7). All populations in the North Dakota and Iowa portions of this ACU are extirpated and only a single isolated population (2017/2018 reintroduction site) remain in Minnesota. Within ACU 251A, 12 metapopulations consisting of 25 subpopulations persist, which represents a 50% decline in the number of metapopulations and a 50% decline in the number of subpopulations (Figures 4.6 and 4.7). Most populations in this ACU are in Northern Manitoba and only two metapopulations are located in Minnesota (although only one of these locations are functioning under a true metapopulation definition). Within ACU 331, 16 metapopulations containing 35 subpopulations persist, which represents 45% and 34% loss of populations, respectively. Within ACU 332, 22 metapopulations and 49 subpopulations persist, which represents a 19% and 11% loss of metapopulations and subpopulations, respectively (Figures 4.6 and 4.7). All populations within ACU 221 have been extirpated.

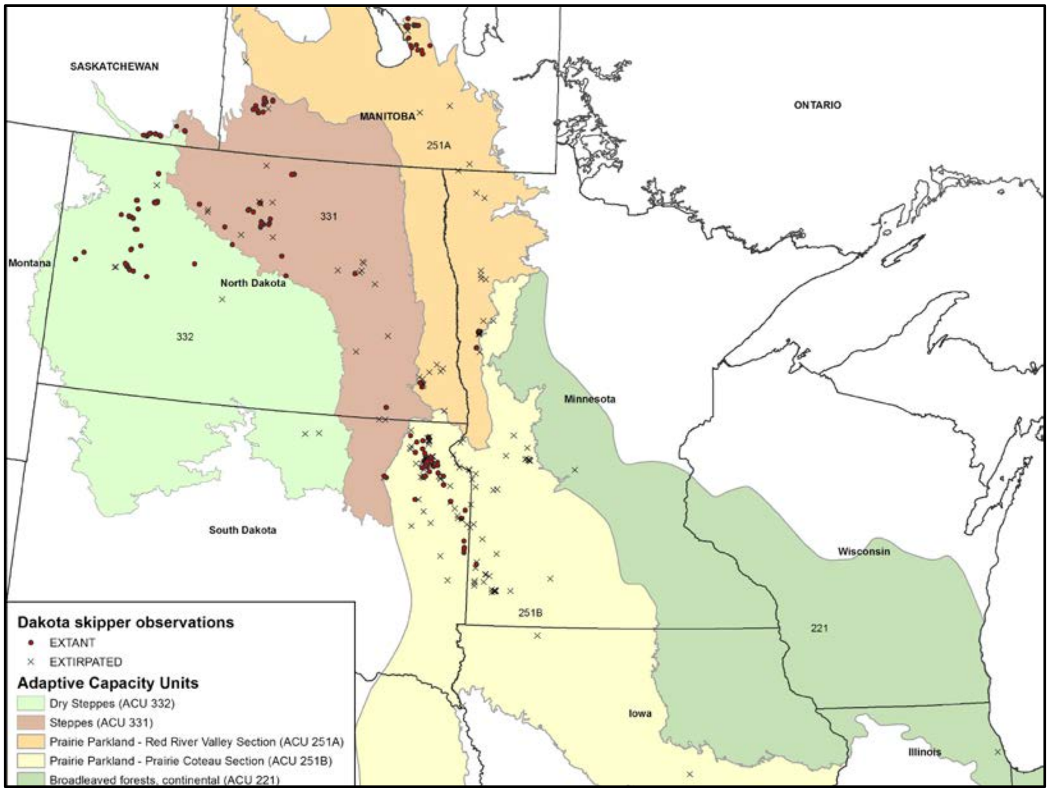


Figure 4.1. The current distribution of Dakota skipper. Red circles represent Dakota skipper sites where presence is extant or unknown, black X's represent sites where the species is no longer present.

Table 4.1. The known number of ACUs and States/Provinces currently occupied by Dakota skipper; the number of extant metapopulations and subpopulations rangewide and by ACU.

	Rangewide	ACU 251A	ACU 331	ACU 332	ACU 221	ACU 251B
ACU	3					
States	5	3	2	2	0	2
Mpopulations	75	12	16	22	0	25
Subpops	156	25	35	49	0	47

Table 4.2. The distribution of current metapopulations and subpopulations within Bailey's Sections (U.S.) and Ecoregions (Canada - A National Ecological Framework for Canada, http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html).

Section/Ecoregion	ACU	# of Meta-populations	# of Sub-populations
Central Dissected Till Plains	251B	0	0
Interlake Plain (Canada)	251A	0	0
Lake Manitoba Plain (Canada)	251A	9	16
North-Central Glaciated Plains	251B	25	45
Red River Valley	251A	2	6
Aspen Parkland (Canada)	331	7	14
Moist Mixed Grassland (Canada)	332	5	11
Northeastern Glaciated Plains	331	13	33
Western Glaciated Plains	331	1	2
Northern Glaciated Plains	332	8	25
Northwestern Great Plains Section	332	6	12
Minnesota & Iowa Morainal and Oak Savannah	221	0	0

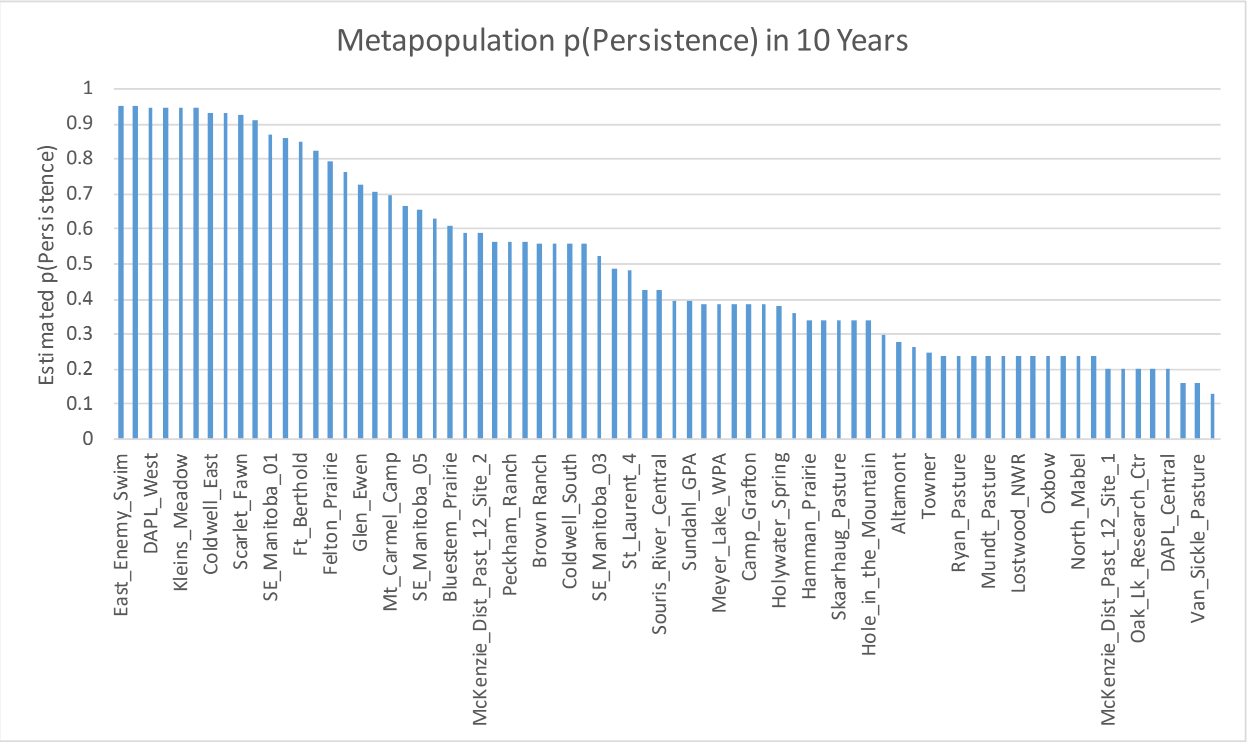


Figure 4.2. Current estimated probability of persistence, pP, in 10 years for each metapopulation. Note, not all populations are displayed. See Appendices for a pP estimates for each population.

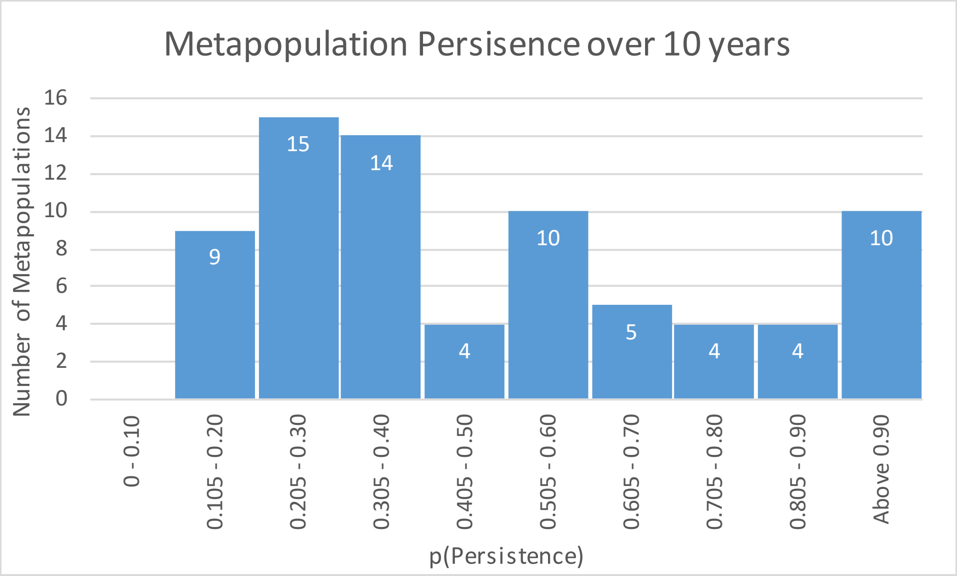


Figure 4.3. The distribution of predicted probability of persistence in 10 years

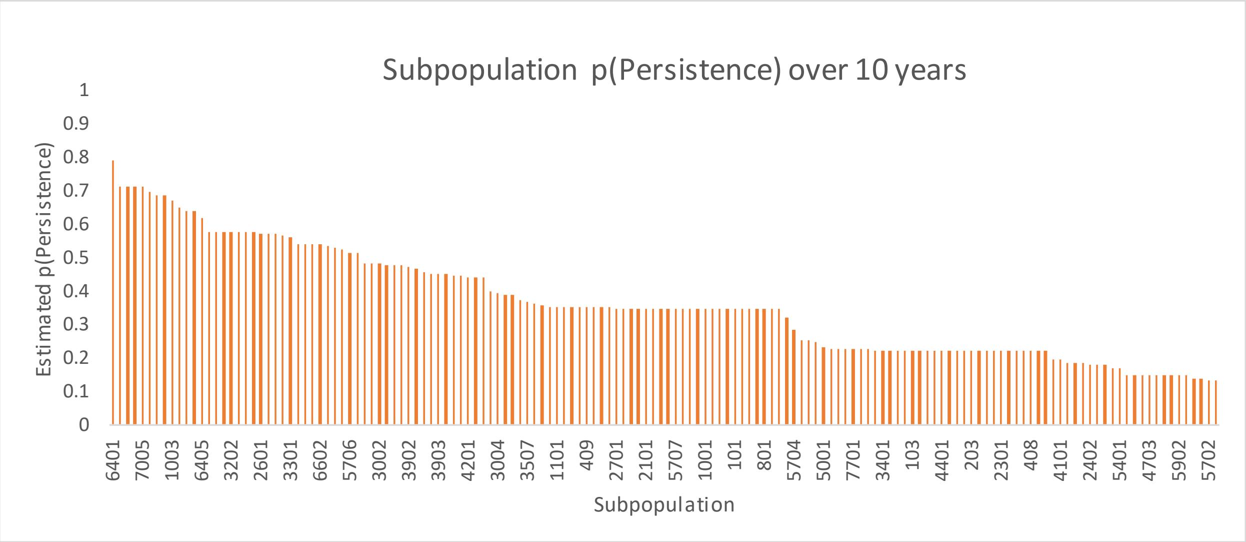


Figure 4.4. Current predicted probability of persistence in 10 years for each subpopulation

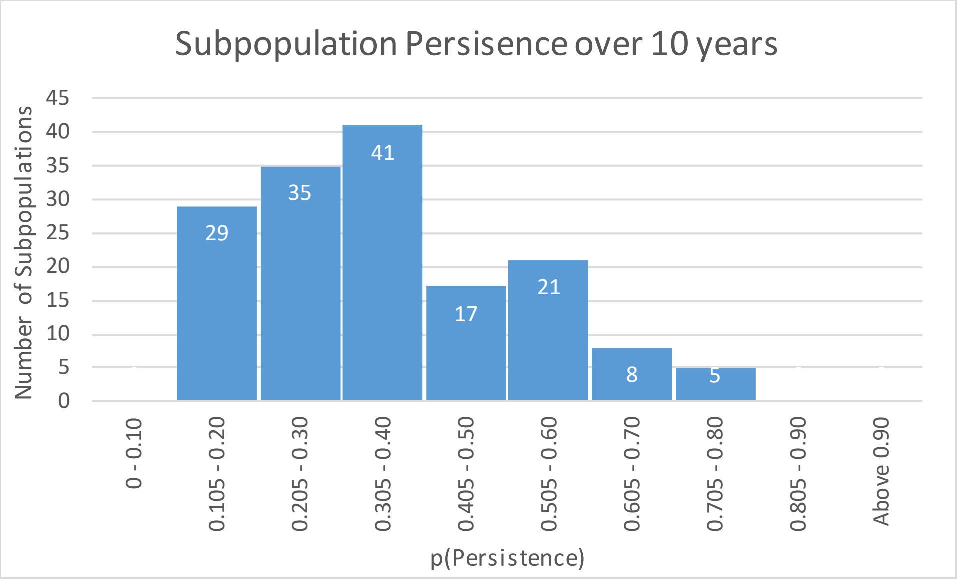


Figure 4.5. The distribution of predicted probability of persistence in 10 years for metapopulations and subpopulations

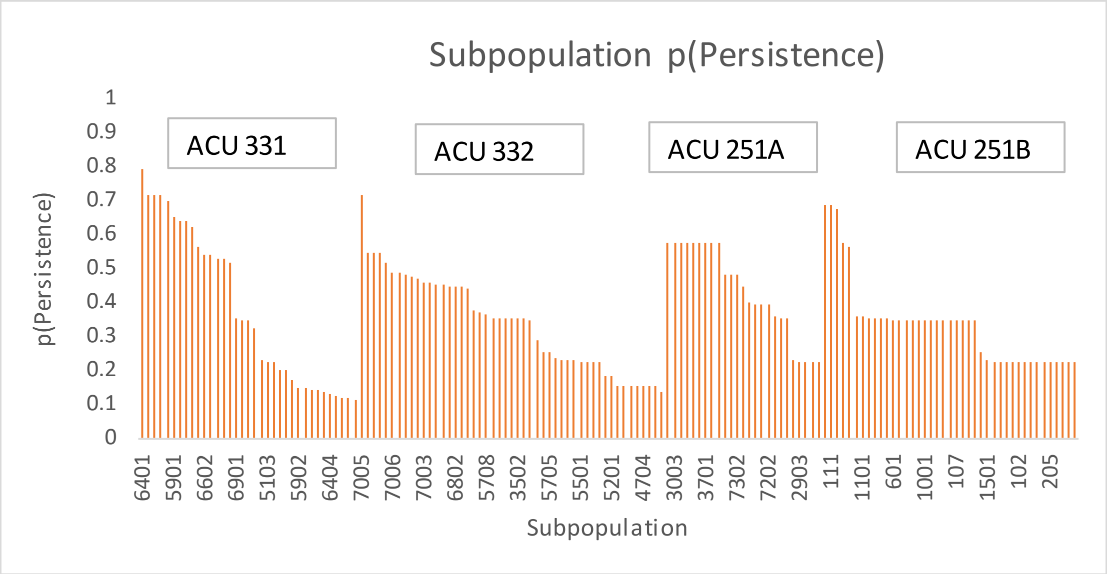


Figure 4.6. Current predicted probability of persistence in 10 years for each subpopulation grouped by ACU

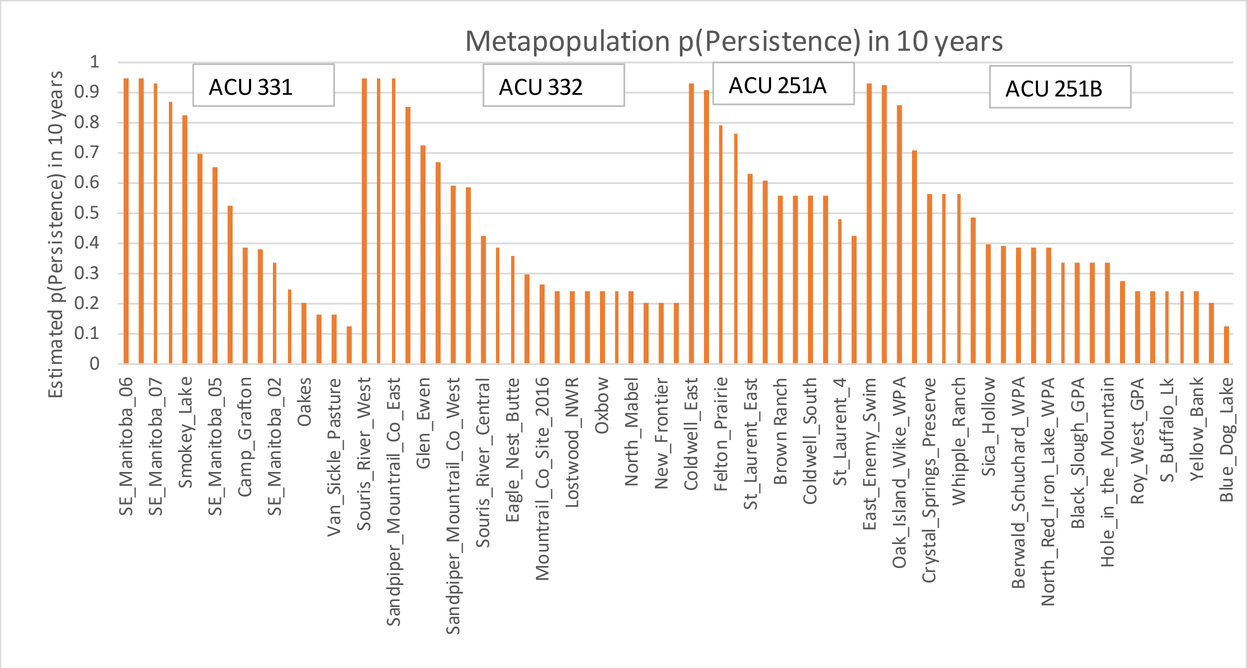


Figure 4.7. Current predicted probability of persistence in 10 years for each metapopulation grouped by ACU; Metapopulation name on x-axis.

Chapter 5. Risk and Supportive Factors

In this chapter, we review the negative and beneficial factors that affected the Dakota skipper historically, are affecting the species currently, and that are likely to affect it in the future. Factors that have a negative impact on Dakota skipper individuals are referred to as risk factors, stressors, or threats; factors that have a beneficial effect are referred to as supportive factors. Collectively, these risk and supportive factors are called influences. In this chapter, we begin by describing the risk factors to Dakota skipper that we could analyze quantitatively and were included in the subpopulation probability of persistence model. We then describe other risk factors that were considered qualitatively and factored into our SSA analysis, together with the subpopulation model results. We discuss the conservation actions that are being undertaken or that should be in light of the species' status and the risks that its populations face.

Loss of native prairie and the degradation of remaining patches of habitat have led to the decline of Dakota skipper and pose continuing threats to the species' continued existence (USFWS 2014). Factors responsible for habitat loss, fragmentation, and degradation that we considered for our SSA analyses include: conversion of native prairie for agriculture or urbanization; ecological succession of native prairie to habitats dominated by brush or trees; invasive species; direct and indirect effects of pesticides, including herbicides; flooding; and land management regimes (grazing, haying, or fire) if done in a fashion that degrade the species' habitat.

5.1 Description of Influences Included in DKS Viability Models

The risk factors below were factored into the Dakota skipper population health model (as described in Chapter 1). Here, we describe the risk factors and summarize the effects on the Dakota skipper and/or its habitat.

Grazing

The impact of grazing on Dakota skipper populations can have both positive and negative influence on Dakota skipper survival. The direction and magnitude of influence depend on the timing, frequency, and intensity as well as on the type of habitat that is being grazed. Grazing may reduce Dakota skipper numbers locally in direct proportion to its intensity due to the reduction in key nectar resources (see Chapter 2), effects to the quality and quantity of larval food plants (see Chapter 2), and perhaps also by influencing adult behavior due to changes in vegetative structure (Dana 1997, p. 4). Monitoring vegetation response of a grazing regime to reach or maintain a desired diversity of vegetation is essential to protecting Dakota skipper habitat.

Briske et al. (2008, p.5) has found that stocking rate is by far the most important variable affecting grazing systems. A compatible stocking rate varies widely depending on the animal, pasture or grass type or composition, and environmental conditions. Stocking rates that are too heavy or season-long grazing result in the removal of forage for Dakota skipper larvae (palatable grass tissue) and adults (nectar-bearing plant parts) in the sort-term; and, such management approaches may result inchanges to vegetation structure and composition in the long-term. This level of grazing may also trample of larvae, alter of larval microhabitats (Royer et al. 2008), and increase non-native species like Kentucky bluegrass (Dekeyser et al. 2015). Years of intense grazing without rest, may preclude recovery, although the capacity for restoration of suitable plant community and other habitat features can be highly variable among sites. Grazing by bison, even when it was locally intense, likely had little or no negative effect on viability of the Dakota skipper historically and even locally the effects were probably only temporary due to both species moving across the landscape (e.g., see England and Devos 1969, p. 88-89).

Despite the aspects of incompatible grazing regimes, rotational grazing can be favorable for Dakota skipper conservation. Dakota skipper populations have been deemed secure at some sites managed with rotational grazing that was sufficiently light to maintain native plant species diversity (Skadsen 1997, pp. 24–29). Grazing may favor key components of Dakota skipper habitat while minimizing mortality compared to prescribed fire (Dana 1991, p. 54, Schlicht 1997, p. 5, Skadsen 1997, pp. 24–29). Grazing may be implemented in 'Type B' habitats, for example, in a manner that leads to high native forb (nectar) species diversity and abundance and foliage heights between 25 and 40 cm (10 and 16 in) that are more conducive to perching and reproductive activities than areas where tallgrasses, such as big bluestem and indiangrass, predominate (Dana 1997, p. 2). In addition, rotational grazing is one of the primary treatments for enhancing native plant diversity, and controlling cool-season invasive grasses (e.g., Kentucky bluegrass, smooth brome*)*, especially where the use of fire may be difficult or undesirable (USFWS 2006, p. 2).

Proximity of nearby populations or contiguous native prairie habitat may alleviate some of the negative impacts of grazing if nearby habitats provide sufficient numbers of immigrants to reestablish the population after habitat quality is restored. Sites should be divided if possible and rotational grazing used in a manner that at least some portion of a site is rested each year and the timing of grazing is varied (USFWS 2016, p.6).

Fire

As with grazing, fire likely affected only a small proportion of Dakota skipper habitat each year historically, allowing for recolonization from unaffected areas during the subsequent flight period (Swengel 1998, p. 83). Accidental wildfires also may burn entire prairie tracts (Dana 1997, p. 15) and may hamper plans to carefully manage Dakota skipper habitat. Prescribed fire can be an important management tool for maintaining or improving native prairie habitat and should be carried out in a way that is compatible with the long-term conservation of the Dakota skipper populations. If not implemented cautiously with respect to its potential effects to the local population or without adequate information on the species local abundance and distribution, it may have significant adverse effects on population health, especially after repeated events (McCabe 1981, pp. 190–191; Dana 1991, pp. 41–45, 54–55; Swengel 1998, p. 83; Orwig and Schlicht 1999, pp. 6, 8).

In Chapter 2 we summarized the general demographic responses that Dakota skippers are likely to exhibit in response to fire, the high sensitivity of the species to fire, and how habitat fragmentation may interact with these factors to threaten affected populations. Some measures may be taken to reduce the level of Dakota skipper mortality during fires, but the health of populations exposed to fire will depend largely on the species' local abundance and distribution before the fire and how those factors intersect with the location and extent of the burned area.

In Chapter 2 we also described why Dakota skipper populations may be categorized as hypersensitive to fire based on the criteria developed by Panzer (2002). In his study, which did not include the Dakota skipper, Panzer (2002) observed mean declines of 67 percent among fire-negative butterfly species, but the author surmised that actual mortality was likely higher due to some immigration into experimental areas after the burn. This underscores a key aspect of how fire may pose a risk to Dakota skipper populations and what factors may determine how they respond after the fire. When all or large portions of a population's habitat are burned, most of the Dakota skippers may die during the fire. If key habitat components are affected positively, including larval plant quantity and quality and nectar availability, post-fire survival of all life stages may increase (e.g., see Warchola et al. 2018). Deterministic factors, including the effects of subsequent management like grazing and the habitat quality of the site, and stochastic factors, such as weather, may limit post-fire population recovery. In addition, the role that immigration from unburned areas plays in the recovery of the species' numbers in burned areas will depend on several factors and is likely to vary widely among sites. Complete extirpation of a population may not occur after a single burn event (Panzer 2002, p. 1306).

The Dakota skipper is not known to disperse widely (Swengel 1996, p. 81; Burke *et al.* 2011, p. 2279); therefore, to reap the benefits of fire to habitat quality, Dakota skippers must either survive in numbers sufficient to rebuild populations after the fire or recolonize the area from a nearby unburned area. In addition, the return interval of fires needs to be infrequent enough to allow for recovery of the populations between burns. Therefore, fire is a threat to Dakota skippers at any site where too little of the species' habitat is left unburned or where patches are burned too frequently.

Haying

As with grazing and fire, haying (mowing grasslands and removing the cuttings) may maintain habitat for the Dakota skipper, but appropriate timing, frequency, and intensity are important. When conducted after eggs hatch (e.g., in August), late-season haying may benefit Dakota skipper populations (McCabe 1981, p. 190). In Manitoba, Dakota skipper populations were more common on hayed prairies than on idle (not hayed) prairies (Webster 2003, p. 10). Haying may cause adults to emigrate if done during the flight period, and haying may reduce nectar availability if done before or during the adult flight period (McCabe 1979, pp. 19–20; McCabe 1981, p. 190; Dana 1983, p. 33; Royer and Marrone 1992, p. 28; Swengel 1996, p. 79; Webster 2003, p. 10).

Hayed prairies are important reservoirs of native prairie plant diversity; however, long-term annual haying negatively impacts prairie plant diversity (Jog *et al*. 2006, pp. 164–165). Jog *et al*. (2006, pp. 164–165) recommended diversifying management to include, for example, periodic fire and to forego annual haying to increase plant species diversity. In a long-term study of a prairie in southeastern Wisconsin, a switch from late-season haying to fire management led to increased native plant diversity and cover of warm-season grasses, although woody plant species also increased (Rooney and Leach 2010, p, 319).).

Lack of Habitat Management

Fire and grazing, along with a highly variable climate, shaped and maintained the pre-settlement tallgrass prairie (Anderson 2006). Although leaving habitat idle does not affect survival of Dakota skippers directly, prairies that lack periodic disturbance become unsuitable for Dakota skippers due to expansion of woody plant species (secondary succession), litter accumulation, reduced densities of adult nectar and larval food plants, or invasion by nonnative plant species (e.g., smooth brome, Kentucky bluegrass) (McCabe 1981, p. 191; Dana 1983, p. 33; Dana 1997, p. 5; Higgins et al. 2000, p. 21; Skadsen 2003, p. 52).

Kentucky bluegrass and smooth brome, which thrive when prairie habitats are left idle for as little as 3-years, arguably pose the greatest risk to native plant composition of Dakota skipper habitats. Native prairies sampled in North Dakota (Murphy and Grant 2005, Grant et al. 2009) and South Dakota (Grant et al. 2009) exhibited deterioration in native prairie vegetation primarily through invasion by smooth brome and Kentucky bluegrass as a consequence of non-disturbance. Once a native plant community is invaded by Kentucky bluegrass or smooth brome, native plant diversity is reduced (Printz and Hendrickson 2015, Toledo et al. 2014, Miles and Knops 2009, Larson and Larson 2010), presumably reducing important larval and nectar plants. Kentucky bluegrass and smooth brome not only affect native plant species cover, they also alter ecological processes such as nutrient cycling, hydrology, and light penetration, and ultimately create self-reinforcing feedbacks, which serve to promote their own dominance (Toledo et al. 2014, Jordan et al. 2008).

Woody species can also encroach in remnant prairie habitats, especially in the wetter, eastern portion and the cooler northern portion of the Dakota skipper range. Briggs et al. (2005) suggest that woody plant expansion is one of the greatest threats to mesic grasslands of the tallgrass prairie ecosystem. Thresholds for cover of woody plants are included in the description of Critical Habitat for the Dakota skipper: "If present, trees or large shrub cover of less than 5 percent of area in dry prairies and less than 25 percent in wet mesic prairies" is needed (USFWS 2015, p. 59272). If not kept “in-check” and woody species can invade prairies, native grasses and flowers are shaded out and displaced. Grassland management becomes increasingly complex when woody vegetation takes hold (Briggs et al. 2005).

Numerous researchers have noted reduced numbers of Dakota skippers at undisturbed sites compared to actively managed sites. For example, Dakota skipper numbers were reduced at Felton Prairie, Minnesota, in tracts that had not been hayed or burned for several years (Braker 1985, p. 47). Another study also observed significantly lower Dakota skipper abundance on unmanaged or idle sites, compared with hayed sites (Swengel and Swengel 1999, p. 285). Skadsen (1997, pp. 10–23; 2003, pp. 8, 35, 42) reported deterioration of several unburned and unhayed South Dakota prairies in just a few years due to encroachment of woody plants and invasive species and found lower species richness of prairie-dependent butterflies and lower floristic quality at sites with no disturbance versus sites managed by grazing or fall haying (Skadsen 2006, p. 3). For example, Dakota skippers returned to an idle site, Pickerel Lake State Park, after a burn conducted in 2007 resulted in a significant increase in forbs, particularly purple coneflower (Skadsen 2008, p. 2). In a separate study, Higgins et al. (2000, p. 24) found that prairie habitats left idle had lower plant diversity and quality than prairies managed with fire. Unless compatible management is instituted, Dakota skipper is unlikely to persist.

Pesticide Use

Pesticide impacts to Dakota skippers are primarily influenced by the extent of the butterfly's exposure to pesticides throughout its range. Pesticides which include herbicides, insecticides, and fungicides are commonly used throughout the Dakota skipper range on crop fields to control plant and animal pests that would otherwise impact yield. Herbicides are also used by conservation agencies and organizations to control weeds in grasslands and native prairies. Pesticides come in many forms: liquid, granular, dust, and as seed coatings and are applied by multiple vehicles such as airplanes and helicopters, farm equipment, ATVs, and on-foot. Timing and frequency of pesticide use varies by type and purpose; however, pesticides are generally used throughout the primary growing season (spring through fall) which coincides with the egg, larvae, pupae, and adult stages of the Dakota skipper life cycle. Due to the loss and fragmentation of native prairie, it is plausible that Dakota skippers can be impacted directly by pesticides by foliar application, and indirectly by exposure to contaminated seed, plant tissue, and soil; as well as consuming contaminated plant tissue. If applicators are not attentive to wind conditions, end-row spacing, droplet size, etc., pesticide drift onto adjacent lands can occur.

Herbicides

Herbicides, in many cases, are used at least once in a growing season to control broadleaf weeds or grasses in crop fields. Herbicides are also commonly used to control woody vegetation and weeds in both public and private grasslands, including native prairie. If not used carefully, herbicides can indirectly impact Dakota skipper populations by eliminating or reducing nectar and foodplants, especially if applied during critical periods of the lifecycle. Adverse effects can occur when herbicides are applied within Dakota skipper habitat or nearby via drift (Dana 1997, p. 3; S. Hedtke, Minnesota Department of Natural Resources, pers. comm. 2015; Stark *et al.* 2012, pp. 25, 27). Herbicide effects are especially impactful when nectar food sources are limited.

Generally, herbicides are thought to be "safe" because the active ingredient/s target plants and not insects. But, the direct effects of herbicide active ingredients on Dakota skipper are not well known, although a few studies exist. Fox (1964) explored effects of five herbicides on numbers of soil invertebrates. Stark *et al*. (2012) evaluated effects of three herbicides on Behr's metalmark (*Apodemia virgulti*) caterpillars. Both studies suggest that any population declines are due primarily to changes in the plant community or from inert ingredients, which are not tested for toxicity.

Herbicides are often mixed with a surfactant (surface active agent that reduces the surface tension of water) and solvents (collectively referred to as adjuvants). Therefore, not only are the skippers exposed to the active ingredient, but also the adjuvants which are oftentimes not included in the risk assessments required for pesticide registration (Mullin et al. 2015, p. 2). Goodwind and McBrydie (2010, p.232) found that 4 of 11 commercially available spray adjuvants were toxic to honey bees at field rates. Furthermore, active ingredients and inert ingredients may interact synergistically, causing impacts that would not occur by exposure to the active ingredients alone (Mullin *et al.* 2015, p. 3). It is plausible that similar impacts from active and inactive ingredients, working together or independently, may cause detrimental impacts to Dakota skippers.

Insecticides

Insecticides are developed solely to kill insects. Most insecticides considered a threat to the Dakota skipper are broad-spectrum in nature; and because larvae of lepidopterans are considered “pests” in agriculture, many insecticides are tested specifically on Lepidopteran species to ensure effectiveness. Therefore, it is likely that Dakota skippers present in areas where insecticide are applied will be killed or otherwise affected. How severely the Dakota skipper is impacted likely depends on the concentration of the insecticide to which it was exposed and/or whether the insecticide became incorporated into plant tissues (e.g. leaves, pollen, nectar) used by the Dakota skipper larvae or adult.

Insecticides registered for use within these systems are represented by three major classes: pyrethroids, organophosphates, and neonicotinoids. Lepidopteran toxicity data are not available for these classes to evaluate the potential magnitude of effects if exposure occurred. However, all three classes have been detected in Dakota skipper habitats (Runquist 2017). The Minnesota Zoo (Runquist 2017) has carried out the only study intended to determine whether pesticides are drifting into Dakota skipper habitat. In 2014, the first year of their study, they detected several insecticides on native grass species used as food plants by the Dakota skipper at sites where the Dakota skipper was present or where the species had recently been extirpated in Minnesota and South Dakota. These included the insecticides chlorpyrifos (an organophosphate) and λ-cyhalothrin and bifenthrin (pyrethroids). They detected each of these insecticides again in 2015 and 2016 and also detected the herbicide Atrazine, the insecticide cypermethrin, clothianidin, a neonicotinoid insecticide, and the fungicide tebuconazole (Runquist 2017). At a Minnesota prairie preserve where the Dakota skipper was reliably detected until at least 2008, levels of chlorpyrifos and λ-cyhalothrin were markedly higher the day after they observed a crop-duster plane spraying insecticide over a soybean field adjacent to the preserve.

Organophosphates and Pyrethroids

Several laboratory studies have examined the toxicity of select organophosphates and pyrethroids to nontarget lepidopteran species within the families Nymphalidae, Lycaenidae, Papilionidae, Hesperiidae, and Pieridae (Salvato 2001, Hoang et al 2011, Eliazar and Emmel 1991, Hoang and Rand 2015, Bargar 2012, Davis et al 1991). In general, while toxicity was exhibited across all species and chemicals, no consistent patterns emerged either within or across studies that demonstrated sensitivity was related to species (or species group), lifestage, or size of adults, though inconsistency in testing regimes may limit the ability to detect patterns that exist.

Neonicotinoids

Neonicotinoid insecticides are neurotoxins that are extremely harmful to invertebrates, causing death by overstimulation. Use of neonicotinoids, especially as crop seed treatments, has grown exponentially both worldwide and in the United States in the last decade (Hladik et al. 2014, Stone 2013). Because of their widespread use and persistence, neonicotinoids are frequently found in the soil, surface and ground water, and air samples (Van der Sluijs et al. 2014, Simon-Delso et al. 2014, Mineau and Palmer 2013).

In turn, this widespread use results in increased risks to nontarget organisms including birds, pollinators, and aquatic invertebrates (Van der Sluijs et al. 2014). Currently, the nonnative honeybee is the primary surrogate used to evaluate risks to nontarget terrestrial insects. In bees, sublethal doses of neonicotinoid insecticides disrupt feeding, foraging growth rate and production of new queens (Mason et al. 2013). In addition, bees exposed at lower doses showed greater susceptibility to pathogens (Mason et al. 2013). Although numerous insecticides may be systemic to some degree, neonicotinoids in particular are known for this characteristic, and are expressed throughout the plant including nectar and pollen of treated crops and plants (Goulson 2013). This means that Dakota skippers at risk through direct contact with neonicotinoid insecticides, but also through their diet.

Flooding

Flooding is a threat to Dakota skippers at sites where too much of the species' habitat is flooded or where patches are flooded too frequently. Flooding can result in loss of habitat by altering the vegetation community or through direct mortality.

Flooding can affect the health of Dakota skipper populations adversely throughout the species' range, although vulnerability to flooding varies significantly depending on habitat type, precipitation patterns, and location relative to creeks, rivers, and lakes prone to flooding. For example, one Dakota skipper population was extirpated when its habitat was "covered by 8 ft. of water during the summer of 1997" as the level of an adjacent lake rose "after several years of above average moisture" (Skadsen 1997, p. 15). The loss of a large area of habitat at two sites in Manitoba, which were previously suitable for Dakota skipper, was caused by prolonged inundation of water that likely caused larval mortality and mortality of suitable nectar and larval food plants (Rigney 2013a, pp. 28, 153). At one of the sites "drainage impediments" exacerbated the flooding and at the other, flooding "of a large area of habitat" was associated with a nearby creek (Rigney 2013, p. 153). The flooding at these sites was part of "considerable flooding" that occurred in 2011 throughout the two regions inhabited by the Dakota skipper in Manitoba due to a "high water table through the winter" and heavy spring rains (Rigney 2013, p. 38). Most "Dakota Skipper sites in Manitoba are in proximity to waterbodies or watercourses and flooding occurs at many sites" (Rigney 2013, p. 160). Royer & Royer (2012) attributed a depression in abundance of Dakota skipper at several North Dakota 'Type A' sites to flooding that occurred in 2011, but they expected numbers to rebound at those sites. More recently at 'Type A' sites in McHenry County, North Dakota, Dakota skipper habitat may be shifting to unsuitable conditions by including more water-tolerant grass species due to rising groundwater (Expert Discussion, May 2017).

Dakota skippers must either survive flooding events in numbers sufficient to rebuild populations after the flood or recolonize the area from nearby habitats that had not flooded. In addition, the return interval of floods must be infrequent enough to allow for recovery of the populations between floods. Changes in hydrology resulting from consolidation wetland draining (agricultural tile drainage) and development may permanently alter the plant community which could result in the loss of larval food and nectar sources.

Habitat Fragmentation and Isolation of Populations

Dakota skipper populations are now scattered in fragments of a once vast grassland ecosystem. Adult Dakota skippers may survive for only a few days, giving them little time to disperse from natal sites (Dana 1991, p. 32). Habitat patches separated by more than 1 km (0.6 mi) may be effectively isolated from one another (McCabe 1981, p. 190; Swengel 1998). Extirpation of small, isolated populations may occur over many years in some cases, but extirpation may be inevitable where immigration from nearby populations is not possible (Hanski et al. 1996, p. 535).

The likelihood of population extirpation may be directly related to the size of habitat fragments. For example, in systematic surveys on Minnesota prairies, Swengel and Swengel (1997, pp. 134–137; 1999, p. 284) found no Dakota skippers on the smallest remnants (less than 20 ha (49 ac)), and significantly lower abundance on intermediate size (30–130 ha (74–321 ac)) than on larger tracts (greater than 140 ha (346 ac)). These differences were unrelated to vegetation characteristics; habitat area did not correlate significantly with vegetation type, quality, or topographic diversity (Swengel and Swengel 1999, p. 284).

5.2 Other Risk Factors Considered in the Analysis

In addition to those risk factors discussed above that we were able to factor into our subpopulation population health model, there are additional risk factors that pose a substantial threat to Dakota skipper populations, but which we were not able to factor into our modeling. These risk factors are qualitatively included in our SSA analyses, along with the quantitative model results, and we include a description of these risk factors here.

Prairie Conversion

Prairie conversion has had a devastating impact on the distribution and abundance of the Dakota skipper historically and, if the rate of prairie conversion increases, it could further exacerbate the threat to the Dakota skipper posed by habitat fragmentation. Conversion of native prairie to cropland and non-agricultural land uses, such as energy development, gravel mining, transportation, and housing, and the degradation of remnant prairie, have reduced the historical abundance and distribution of the Dakota skipper and pose continuing threats to the species' persistence.

Prairie conversion is the act of replacing native prairie plants with non-native grasses or legumes for hay or pasture, crops, or other developments. This conversion increased dramatically in the U.S. with the invention of the steel plow, making it easier to cut through heavy sod grasses. The historical loss of tallgrass prairie over the range of the Dakota skipper varies from about 85% in South Dakota to nearly 100% in Iowa, Minnesota, and North Dakota (Samson and Knopf 1994). Similarly, though not as drastic, about 60% of mixed grass prairies in South and North Dakota and Montana have been converted to cropland (Higgins et al. 2002).

Following the rapid and extensive conversion of native prairie that began in the 1800s, conversion of remnant native grasslands continues today and threatens to further deplete Dakota skipper habitat. It is unclear how much is converted annually due to differences in the geographic area or time period studied. Earlier studies estimate an annual conversion rate of

0.004% in the Missouri Coteau region of central North Dakota and north-central South Dakota, from 1989-2003 (Stephens et al. 2008) and 1% in the Northern Great Plains from 1997-2007 (Classen et al. 2011). Conversion rates documented in more recent studies reflect the increase in corn prices that occurred in 2007. Wright and Wimberly (2013) estimated the annual rate of conversion in the Western Corn Belt was between 1%-5.4% and Gage et al. (2016) reported a 2% annual loss from 2009-2015 in the Great Plains.

Although corn prices have decreased in recent years, conversion most likely will continue at a significant rate due to ethanol fuel standards, crop insurance subsidies or other governmental disaster or loan programs, as well as technological advances in equipment, seed, and herbicides (Classen et al. 2011, Wright 2015, Higgins et al. 2002). The region with the greatest grassland conversion currently occurring is the area covered by the Prairie Habitat Joint Venture[2], which covers portions of the Canadian provinces of Manitoba, Saskatchewan, and Alberta (Gage et al. 2016). From 2011-2015, cumulative losses in this region alone totaled 16.44% with an average of over 4% per year. This area contains important Dakota skipper populations in southeastern Saskatchewan and southwestern Manitoba. Similarly, the Prairie Pothole Joint Venture region[3], which contains all the remaining Dakota skipper populations in the United States, is experiencing sustained grassland conversion. During the same period (2011-2015), more than 10% of this region's grasslands had been converted to cropland with an average annual loss of 2.7% (Gage et al. 2016). The proportion of these grasslands that were Dakota skipper habitat is unknown. Dakota skippers inhabit only high quality native prairies; when converted they are essentially lost as habitat for the species, even if they are later replanted to grassland. This has been documented by looking at the survey data over time and from expert observation at prairie sites bordered by a completely re-established prairie.

Additional conversion and fragmentation of native prairie may result from the ongoing development of wind energy in the Dakota skipper range. There are currently seventeen wind farms located in the eastern half of South Dakota with 34 more proposed (SDWEA 2015). Although wind towers probably do not cause direct mortality (e.g. through collision) of butterflies (Grealey and Stephenson 2007), the area affected by the development of a wind energy farm can be significant. For example, a 200+ turbine proposed wind farm in Clark County South Dakota would be spread across 43,000 acres of land (C. Mueller, U.S. Fish and Wildlife Service, Waubay National Wildlife Refuge, *pers. comm.* 2017). Not all the area will be directly affected, but development of pads, access roads, and collection lines will occur in grasslands, some of which are native prairie. This will not only result in a direct loss of native prairie, but it will also increase grassland fragmentation and can exacerbate the invasion of non-native species (Jones et al. 2015). In the Draft Environmental Assessment of the Crocker Wind Farm, a desktop review of appropriate Dakota skipper habitat identified 65 potential areas for surveys. Ground based assessments found 34 sites with suitable habitat. These 34 sites were surveyed from 29 June to 13 July 2017 for presence of Dakota skippers and Poweshiek skipperlings with negative results for either species (Crocker Wind Farm, LLC 2018). The Peckham Ranch metapopulation is within 6.5 miles of the Crocker Wind Farm and currently six SD metapopulations occur within the boundaries of proposed wind farms and three more are within 5 miles, including Scarlet Fawn and Oak Island/Wike metapopulations. North Dakota,

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[2] See https://www.phjv.ca/

[3] See http://ppjv.org/

South Dakota and Minnesota all occur in high wind areas (USDOE 2018) and will likely continue to develop wind energy resources.

Climate Change

Climate change may currently or into the future pose a threat to the Dakota Skipper. Although experts believe climate change effects could—currently or over time--influence Dakota skipper survival or reproductive success, data are lacking. Given that climate, along with fire and herbivory, were major drivers in maintaining the native plant cover prior to Euro-American settlement (Anderson 2006), we explored the effects of climate change via changes to habitat. Specifically, we evaluated how length of growing season and annual precipitation are predicted to change over time (1950-2100) under two IPCC Representative Concentration Pathways (RCP) scenarios, RCP 4.5 and RCP 8.5.

Growing Season Length

Under the RCP 4.5 and 8.5 scenarios, all four ACUs show an increasing trend in growing season length. Cool-season invasive grasses, such as Kentucky bluegrass and smooth brome, threaten to become more dominant in native grassland plant communities and to form nearly monotypic stands in some areas. An increase in growing season length equates to “added days” either in early spring or late fall when Kentucky bluegrass (Uchytil 1993) and smooth brome are photosynthetically active. According to John Hendrickson, Agricultural Research Service *(pers. comm. 2018)*, data collected at the Agricultural Research Service Station at Mandan, ND indicate that in the 1990's precipitation increased by 25%, and in the 2000's increased 10-15%, with the growing season being extended primarily in the fall. Smooth brome and Kentucky bluegrass can take advantage of longer falls because of their ability to regrow as temperatures drop and day length decreases. Also, these two invasive grass species photosynthesize earlier than native cool-season grasses in the spring (DeKeyser et al. 2015, Stubbendieck et al. 1992), allowing for increased invasion opportunities if earlier springs occur under climate change.

As a result of longer growing seasons, Type A habitats in the Steppes ACU (ACU 332) may experience greater invasion from Kentucky bluegrass and smooth brome than Type B habitats (found in the remaining three ACUs) due to the moist prairie soils and low topographic relief in the Steppes ACU. Kentucky bluegrass is a hydrophilic, drought-intolerant grass (Jackson et al. 2002, Uchytil 1993) and is adapted for growth in cool, humid climates (Uchytil 1993). According to Printz and Hendrickson (2015), many native plants present on ecological sites with very droughty soils and limited organic matter (i.e. very shallow or shallow gravel) tend to maintain a more diverse native component because native plants possess adaptations giving them a competitive edge over invasive species such as Kentucky bluegrass and smooth brome. However, adjoining sites with more productive soils (i.e., wetter, usually lower in the landscape profile) often become Kentucky bluegrass and smooth brome-dominated.

Considering Dakota skipper habitat, once a native plant community is invaded by Kentucky bluegrass or smooth brome, native plant diversity is reduced (Printz and Hendrickson 2015, Toledo et al. 2014, Miles and Knops 2009, Larson and Larson 2010), presumably reducing target larval and nectar plants. Kentucky bluegrass and smooth brome not only affect plant species cover, they also alter ecological processes such as nutrient cycling, hydrology, and light penetration, and ultimately create self-reinforcing feedbacks, which serve to promote dominance (Toledo et al. 2014, Jordan et al. 2008).

Short-term and Long-term Precipitation

In all four ACUs under RCP 4.5, the annual precipitation trend is stable to slightly decreasing, while under the RCP 8.5 scenario, annual precipitation in all four ACUs increases. This stable-to-decreasing trend under RCP 4.5 *could* be beneficial when considering invasion of cool-season exotic grasses such as Kentucky bluegrass, which is associated with abundant annual precipitation (Stubbendieck et al. 1985, Hardy BBT Limited 1989). The decreasing trend may not be significant enough to shift the competitive edge back to native prairie plants without human intervention (i.e., prescribed burning and grazing). However, prescribed fire and prescribed grazing behave differently on sites dominated by cool-season exotic grasses compared to native plant dominated sites. There are numerous data gaps associated with reducing Kentucky bluegrass and smooth brome and understanding how management treatments such as burning and grazing behave under invasion scenarios. Likely, the timing of treatments, along with short-term and long-term precipitation are factors that will affect a land manager's ability to increase native plants. Based on recent data analysis, we do know that different treatment (i.e., burning, grazing, and rest) outcomes are affected by prior year precipitation (Moore et al. 2018). In the mixed grass prairie, when prior year precipitation was wetter than average, it appears that burning and grazing treatments were more effective at increasing native plants compared to when prior year precipitation was drier than average (Moore et al. 2018). Considering long-term precipitation, data show that warmer and wetter areas of the prairie pothole region currently have increased invasion of cool-season exotic grasses; comparatively, cooler and drier areas of the prairie pothole region possess higher percentages of native plant cover than the former (Moore et al. 2018).

Some studies suggest a possible east to west shift in the forest-prairie transition zone due to increasing suitability for woody species to inhabit what is currently grassland and shrubland (Bachelet et al. 2003). The primary drivers in this "tension" between prairies and forest are climate, soils and topography (Andersen 2005). There is evidence that woodlands existed along riparian areas, wetland edges, on escarpments, and sand hills prior to Euro-American settlement (Severson and Sieg 2006; Grant and Murphy 2005). These trees and shrubs existed because of wetter soils and protection from the wind; however, spread of woody plants was limited primarily by drought, flood, fire, and herbivory (Severson and Sieg 2006). Extirpation of bison, fire suppression, tree plantings (Grant and Murphy 2005), and wet cycles in recent years have allowed for the expansion of woody vegetation. As an example, at J. Clark Salyer National Wildlife Refuge (North Dakota), the cover of aspen woodland has double since European settlement. With this continued encroachment, it is possible that remaining grasslands could be lost within 75-130 years, eliminating habitat for grassland obligate species such as the Dakota skipper (Grant and Murphy 2005), especially under the 8.5 scenario. It is possible that a slightly decreasing precipitation trend in all four ACUs could indirectly benefit Dakota skipper habitats by creating lengthier windows for management of woody vegetation; however, it is highly likely that managers would not be able to keep up with removing woody invasion.

Although warming may occur throughout the range of the Dakota skipper, temperatures in northwest Minnesota (Forest-steppes ACU), and northeast North Dakota, Saskatchewan and

Manitoba (Steppes ACU) may remain cool enough that an increase in annual precipitation under the RCP 8.5 scenario would still be conducive to tree and shrub expansion and a concomitant tendency to shrink Dakota skipper habitat patches. Once woody species invade prairies and their density increases, native grasses and flowers are shaded out and displaced. The understory is either somewhat barren or replaced with cool season exotic grasses such as Kentucky bluegrass and smooth brome. Grassland management becomes increasingly complex when woody vegetation takes hold (Briggs et al. 2005). Under this scenario, Dakota skipper habitats are likely to degrade quickly, especially if not managed (i.e. rested; Briggs et al. 2005).

5.3. Catastrophes

Influences generally lie along a continuum of impact from no influence on reproductive potential and survival to population collapse. The latter are events we term 'catastrophes.' We analyzed two potential catastrophic events: extreme drought and widespread pesticide spray.

Catastrophic Drought

Drought is a natural ecosystem process of prairies, and prairie-dependent species are generally very drought tolerant. Through expert input, we defined catastrophic drought as a Palmer Drought Severity Index of -4.0 or lower, persisting for one year or more (i.e., one full generation). The primary effects of this level and extent of drought include direct mortality through larval desiccation, as well indirect mortality (e.g., starvation) resulting from impacts to larval plant food resources. Extreme drought would cause above-ground plant tissues to desiccate, resulting in lower quality and availability of larval food and water resources (R. Dana, Minnesota Dept. of Natural Resources, *pers. comm.* 2016; R. Westwood, University of Winnipeg, *pers. comm.* 2016). Larvae are most susceptible to drought mortality during late summer and winter (R. Royer, retired, Minot State University, *pers. comm.* 2016). Adults in captivity require the provision of a water source, such as freshly cut flowers or misting of cages (R. Dana, Minnesota Dept. of Natural Resources, *pers comm.*, 2017; E. Runquist, Minnesota Zoo, *pers comm. 2017*), indicating that severe droughts during mid-summer (i.e., the flight period) could result in direct adult mortality. The negative effects of drought would be particularly strong in dry prairies (Royer et al. 2008 referred to these as Type B Habitats), though a catastrophic drought could cause metapopulation collapse in any prairie type.

A milder or shorter-lived drought may have any one of the above effects (e.g., reduced larval food quality) without leading to population collapse. The species experts agreed that the duration and extent of the drought would need to be extreme in order to cause extirpation of this prairie-dependent (i.e., drought tolerant) species.

Catastrophic Pesticide Events

A catastrophic pesticide event is conceivable given the increased occurrence of invasive species. Participants from a recovery planning workshop identified the potential for a widespread response to an invasive pest outbreak as a plausible and concerning potential event. Our analysis did not take this possible catastrophe into account, but given the concerned raised, it is an event that should be addressed in recovery planning moving forward.

Stressor Summary

Based on our population-specific analysis, the predominant stressor is habitat destruction followed by biocide use, with 71% and 58% of metapopulations affected by habitat loss and biocides, respectively (Figure 5.1). In the Prairie Parklands (ACU 251A/251B), 21 and 18 metapopulations are negatively affected by habitat destruction and biocide use, respectively; a few populations are being negatively affected by unfavorable haying and grazing practices (Table 5.1). Within the Steppes province (ACU 331), the majority of populations are also negative affected by habitat destruction and biocide use; with only 2 metapopulations impacted by unfavorable grazing practices (Table 5.1). Within the Dry Steppes ACU (332), 7 and 6 metapopulations are exposed to habitat destruction and biocides stressors (Table 5.1).

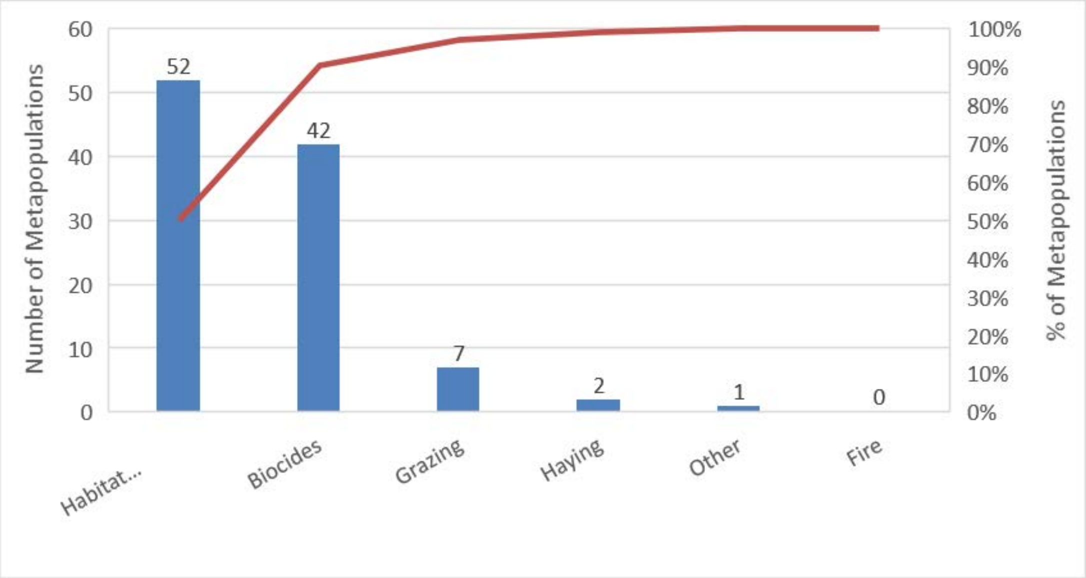


Figure 5.1. The number (primary axis) and percent (secondary axis) of metapopulations affected by various influences (x-axis).

Table 5.1. The number of metapopulations exposed to stressors.

	Habitat Destruction	Haying	Grazing	Fire	Biocides	Other
Rangewide	52	2	7	0	42	1
ACU 285	21	2	5	0	18	0
ACU 296	24	0	2	0	18	1
ACU 304	7	0	0	0	6	0

5.3 Supportive Factors

Supportive factors specifically focused on the Dakota skipper are few. In 2014, the Dakota skipper was listed as Threatened under the ESA. In Canada, Dakota skipper is listed as threatened on the SARA List of Wildlife Species at Risk. States that recognize Dakota skipper in their State Wildlife Action Plans as Endangered, Threatened or Greatest Conservation Need include Minnesota, North Dakota, South Dakota, and Iowa.

The Dakota skipper was listed in 2014 and thus is protected under the ESA; federal agencies are required under section 7(a)(2) of the ESA to consult with the Service and ensure their activities (including those they conduct themselves as well as those they may fund, authorize or permit) do not jeopardize the continued existence of the species. The conservation focus in the section 7(a)(2) consultation process is often limited to avoidance and minimization of impacts of activities subject to federal purview, not necessarily on actions to broadly improve the status of the species. However, most of the extant Dakota skipper populations are located on private land (about 70%); about 13% are on State or county owned land, and about 17% are on Federal or Tribal lands in the U.S. and over 90% of the populations are located on private land in Canada. Most conservation for Dakota skipper will take place on private lands; conservation actions by Non-governmental organizations, County and State governments, and private landowners are occurring, but not in a coordinated manner. We anticipate recovery of the species will be predicated on a comprehensive, coordinated strategy that we will be designing together with our Federal, Tribal, State and local partners. Below we describe some of the ongoing conservation efforts.

Maintenance of High Quality Habitats

Recovery of the Dakota skipper will be closely tied to the extent and condition of its native grassland habitat. The species is endemic to North American tallgrass and mixed grass prairie and does not inhabit non-native grasslands, weedy roadsides, tame hayland, or other habitats that are not remnant native prairie. In addition, Dakota skippers have not been recorded in reconstructed prairie, e.g., former cropland that has been replanted to native prairie. Therefore, Dakota skipper needs native prairie habitats that are diverse in flowering herbaceous plants and native grasses.

Land management actions that affect Dakota skipper habitat will also play a critical role in the species' survival. Haying, grazing, and fire are essential management tools to maintain native prairie and the essential features of the Dakota skipper's grassland habitats. In the absence of grazing, fire, or haying, Dakota skipper habitat is likely to become too brushy or wooded to support the species (e.g., Rigney 2013, p. 151) or can succumb to invasion by cool season exotic grasses, especially Kentucky bluegrass and smooth brome. Increasingly, conservation land managers are considering Dakota skipper and other invertebrates in setting their management regimes (timing, intensity and duration of the management practices).

Research and Captive Rearing

The captive rearing program at Minnesota Zoo is now capable of producing significant numbers of the Dakota skipper ex situ, such that reintroduction of the species is feasible. The Minnesota Zoo, U.S. Fish and Wildlife Service and its partner agencies have finalized a plan to guide ex situ management of the species. Under that plan, ex situ management would be used to facilitate important research, but also to produce animals for reintroduction. In May 2017, a formal plan for the reintroduction of Dakota skipper at Hole-in-the-Mountain Prairie was prepared and the first year of introduction was conducted during the 2017 flight season. There were 196 individuals released at Hole-in-the-Mountain Prairie and 111 were observed post-release. Mating, oviposition in the wild, and egg viability have all been confirmed and two additional years of Dakota skipper release are planned at this site followed by extensive monitoring to determine if the population is self-supporting (Runquist and Nordmeyer 2018).

Perpetual Protection of Dakota Skipper Habitats

Acquisition of perpetually protected lands throughout the Dakota skipper's range has been ongoing for many decades. Grasslands are protected both through fee title and easements, by many agencies and organizations. In recent years, native prairie protection and management has become a high priority for many of those agencies. For example, several conservation agencies in Minnesota are committed to a unified, 25-year statewide prairie conservation plan, which includes goals for perpetual protection of over 850,000 acres of grasslands in targeted landscapes (Minnesota Prairie Plan Working Group 2011).

Although the condition of these protected grasslands is not fully known, it is likely that at least some of these conservation lands and easements include good to high quality native prairie and could provide habitat for Dakota skippers. At the least, these acres may provide areas for dispersal and connectivity between populations.

Chapter 6. Analysis of Future Conditions

In this chapter, we describe our analysis of the future condition of Dakota skipper. Specifically, we forecast the probability of persistence of the subpopulations and metapopulations over 10 years given future state conditions (Note, the estimates for persistence are 20 years out as the future state conditions are 10-year projections and the probability of persistence estimates are 10-year projections beyond the future state conditions).

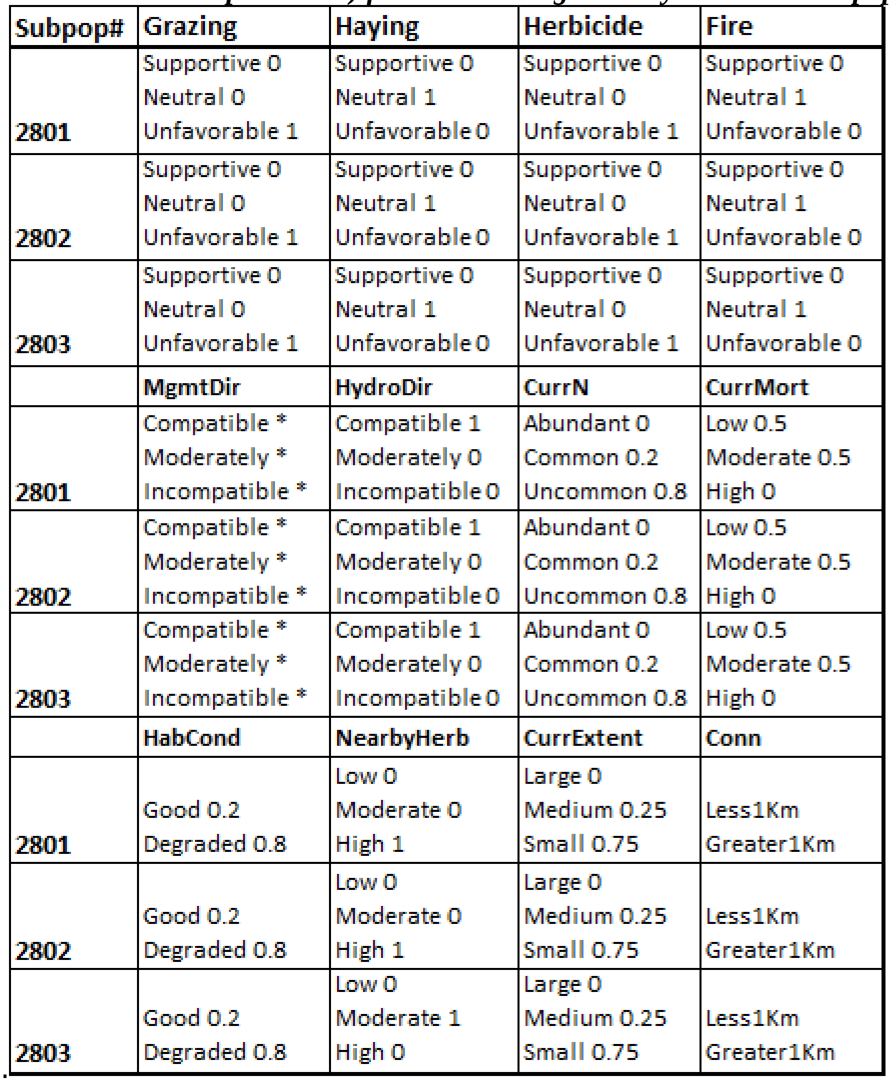
To assess the population into the future, we devised plausible future scenarios. To capture the range of realistic future conditions, we modeled three different scenarios for each metapopulation: a) best-case; b) worst-case; and c) most likely-case. A narrative summary of these scenarios and specific model inputs are available upon request. An example using the Brookings_Co_Pastures metapopulation is provided below.

How we modeled future scenarios, utilizing Brookings_Co_Pastures Metapopulation as an example: *Three subpopulations make up this metapopulation that follow a ridge of potential habitat to the north and south. One subpopulation, Brookings Co Private Pasture, is still considered extant, although the site was last surveyed in 2006 and follow up surveys are not anticipated given the ownership status. The other two sites (Coyote Ridge - South and Coyote Ridge - North), located to the north are proposed for wind development and a portion of the available habitat has been surveyed with positive detection in 2009 and negative detection in 2017. The subpopulations are from 3,400 m to 3,700 m (2.1-2.3 miles) apart. The next closest metapopulation is Oak Lake Research Center, which is 8,500m (5.3 mile) to the north. All three subpopulations have extensive acreage but grazing pressure at these locations has resulted in a decrease of floral diversity. Coyote Ridge – North appear to have the more substantial population of Dakota skippers, but actual numbers were not quantified. Private pastures vary from fair to poor and most skippers were observed within ROW's or fence lines where cattle could not get to, although extensive surveys of the grazed areas were not conducted.*

Best-case Scenario - *Remaining grasslands are brought into protected ownership and rotational grazing implemented to improve pastures. This metapopulation exists on sites with frequent grazing, but the topography in the area has protected agriculture development thus far so any habitat that can be protected is important.*

Worst-case Scenario - *All three sites are unprotected grasslands and may further be fragmented by agriculture or wind development reducing the habitat available. Grazing on pastures continue at a high intensity and further reduce nectar sources, possibly increasing non-native species due to less available competition.*

Table 6.1. The 'current' input values) for the Brookings County Pastures metapopulation



Subpop#	**Grazing**	**Haying**	**Herbicide**	**Fire**
2801	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0
2802	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0
2803	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0	Supportive 0 Neutral 0 Unfavorable 1	Supportive 0 Neutral 1 Unfavorable 0
	MgmtDir	**HydroDir**	**CurrN**	**CurrMort**
2801	Compatible * Moderately * Incompatible *	Compatible 1 Moderately 0 Incompatible 0	Abundant 0 Common 0.2 Uncommon 0.8	Low 0.5 Moderate 0.5 High 0
2802	Compatible * Moderately * Incompatible *	Compatible 1 Moderately 0 Incompatible 0	Abundant 0 Common 0.2 Uncommon 0.8	Low 0.5 Moderate 0.5 High 0
2803	Compatible * Moderately * Incompatible *	Compatible 1 Moderately 0 Incompatible 0	Abundant 0 Common 0.2 Uncommon 0.8	Low 0.5 Moderate 0.5 High 0
	HabCond	**NearbyHerb**	**CurrExtent**	**Conn**
2801	Good 0.2 Degraded 0.8	Low 0 Moderate 0 High 1	Large 0 Medium 0.25 Small 0.75	Less1Km Greater1Km
2802	Good 0.2 Degraded 0.8	Low 0 Moderate 0 High 1	Large 0 Medium 0.25 Small 0.75	Less1Km Greater1Km
2803	Good 0.2 Degraded 0.8	Low 0 Moderate 1 High 0	Large 0 Medium 0.25 Small 0.75	Less1Km Greater1Km

Rangewide Forecasted Condition

The probability of persistence estimates for each metapopulation are provided in Figure 6.1 for the best-case and worst-case scenarios. There are only slight differences between the two scenarios, and thus to save space, we provide the results for the two extremes scenarios in Figure 6.2 (best-case and worst-case) and not the most likely-case scenario. Under both scenarios, the just over half of the metapopulations have a predicted probability of persistence of less than 0.50 and 10 metapopulations have predicted probabilities of persistence greater than 0.90 (Figure 6.2).

As explained in Chapter 4, our model assumes functional connectivity between subpopulations. Many of the metapopulations are, however, fragmented and thus, the predicted persistence estimates are likely optimistic. We can garner further insights about metapopulation health by looking at the health of the underlying subpopulations. Again, there is not much difference between the best-case and worst-case scenarios (Figure 6.3). Under both the best-case and worst-case scenarios, the majority (78% and 79% under the best-case and worst-case scenarios, respectively) of the subpopulations have probability of persistence less than 0.50 (i.e., less than 50% chance of surviving over the next 20 years), and none of the subpopulations have probability of persistence greater than 0.70 (Figure 6.4).

Adaptive Capacity Unit Forecasted Condition

The probability of persistence estimates grouped by ACU is provided in Figures 6.5 and 6.6 for the best and worst-case scenarios. There are only slight differences between the two scenarios (see Figure 6.5). Within ACUs 331, 332 and 251B, half to 68% of the metapopulations have predicted probabilities of persistence less than 0.50, and only 2 or 3 of the metapopulations have persistence estimates greater than 0.90 (Figure 6.5). Within ACU 251A, 2 of the 12 metapopulations (17%) have less than 0.50 probability of persistence and have greater than 0.90 probability of persistence. More than half of subpopulations in all ACUs have less than a 50% chance of surviving over the next 20 years, with 89% and 90% of subpopulations in ACUs 251B and 332, respectively, having less than 0.50 probability of persistence (Figure 6.6). None of the ACUs have subpopulations have more than 80% chance of persisting (Figure 6.6).

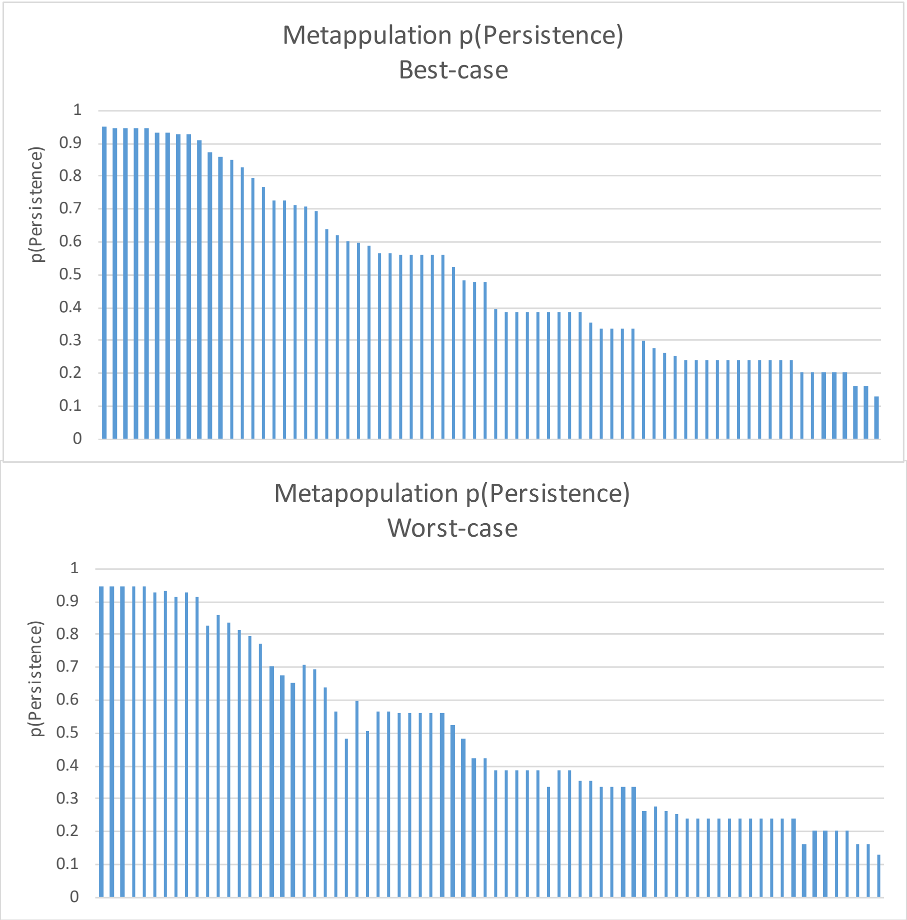


Figure 6.1. The predicted probability of persistence in 20 years for all extant and unknown metapopulations under the best-case and worst-case scenarios (metapopulation name on the x-axis; Note, not all metapopulation names are listed due to space)

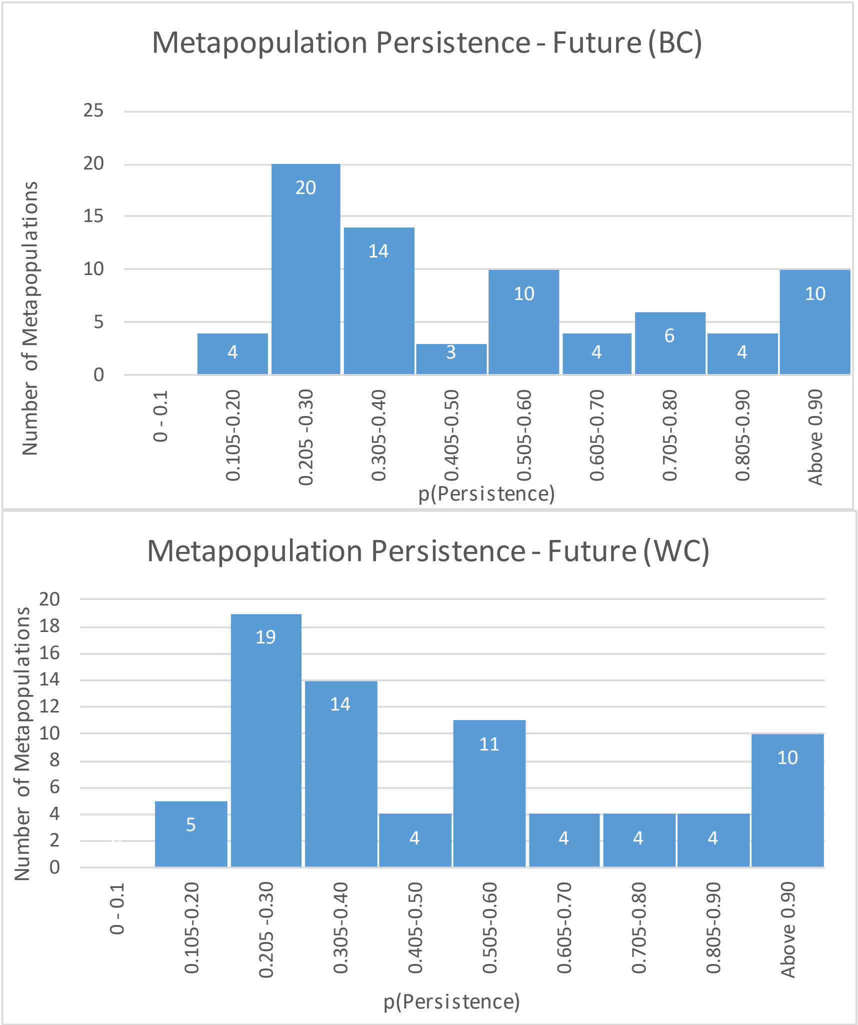


Figure 6.2. The distribution of predicted probability of persistence in 20 years for metapopulations under the worst-case (WC) and best-case (BC) scenarios

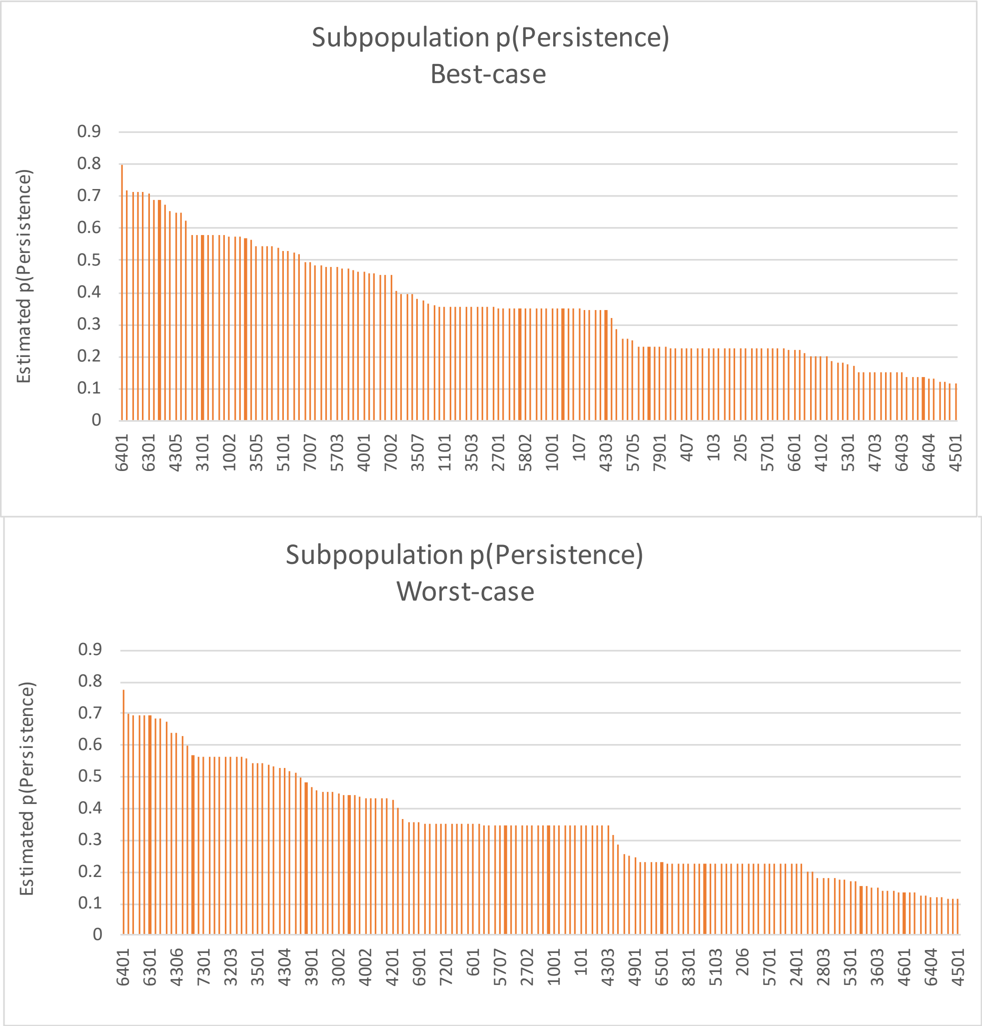


Figure 6.3. The predicted probability of persistence in 20 years for all extant and unknown subpopulations under the best-case and worst-case scenarios

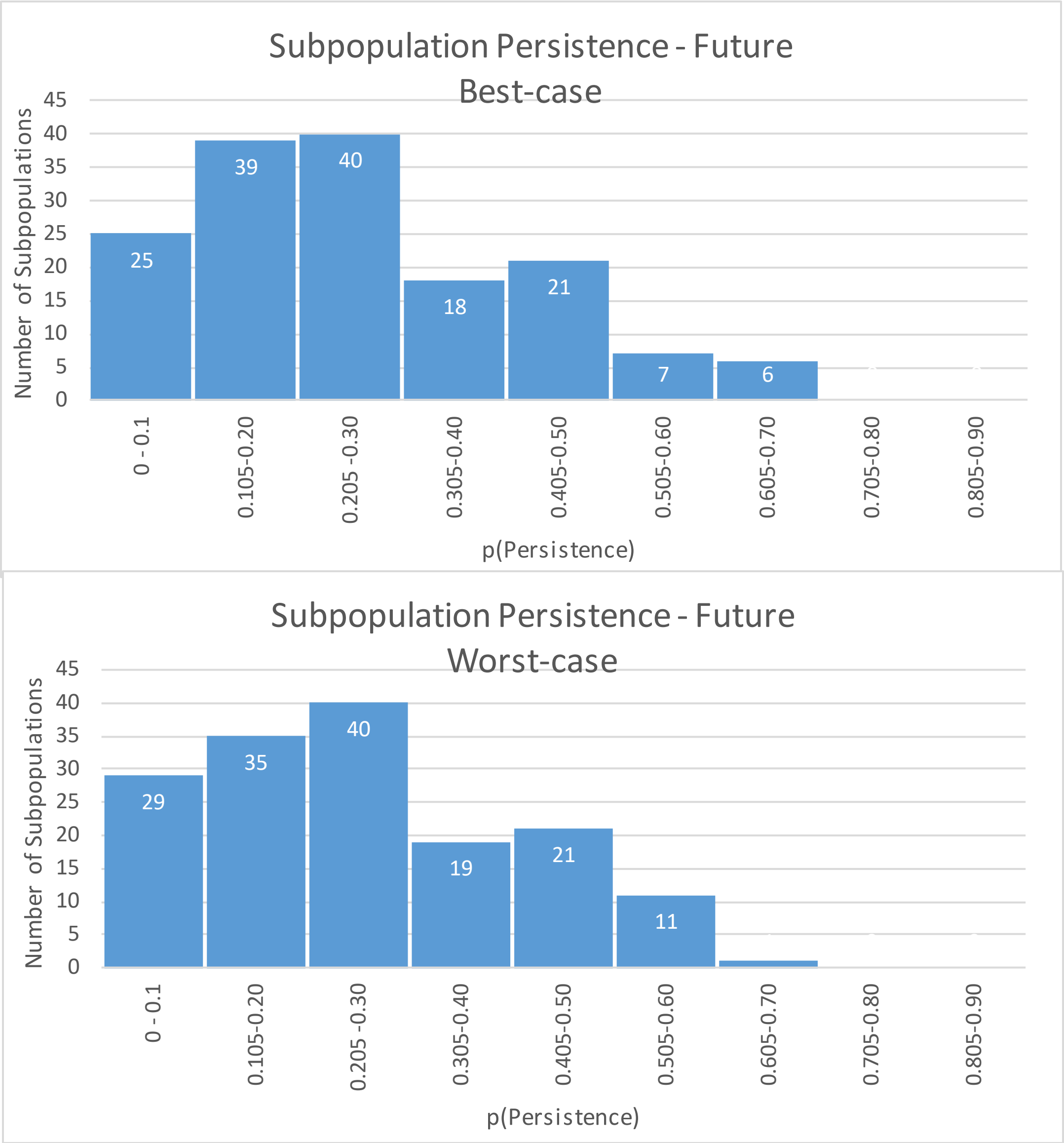


Figure 6.4. The distribution of predicted probability of persistence in 20 years for all subpopulations under the worst-case (WC) and best-case (BC) scenarios

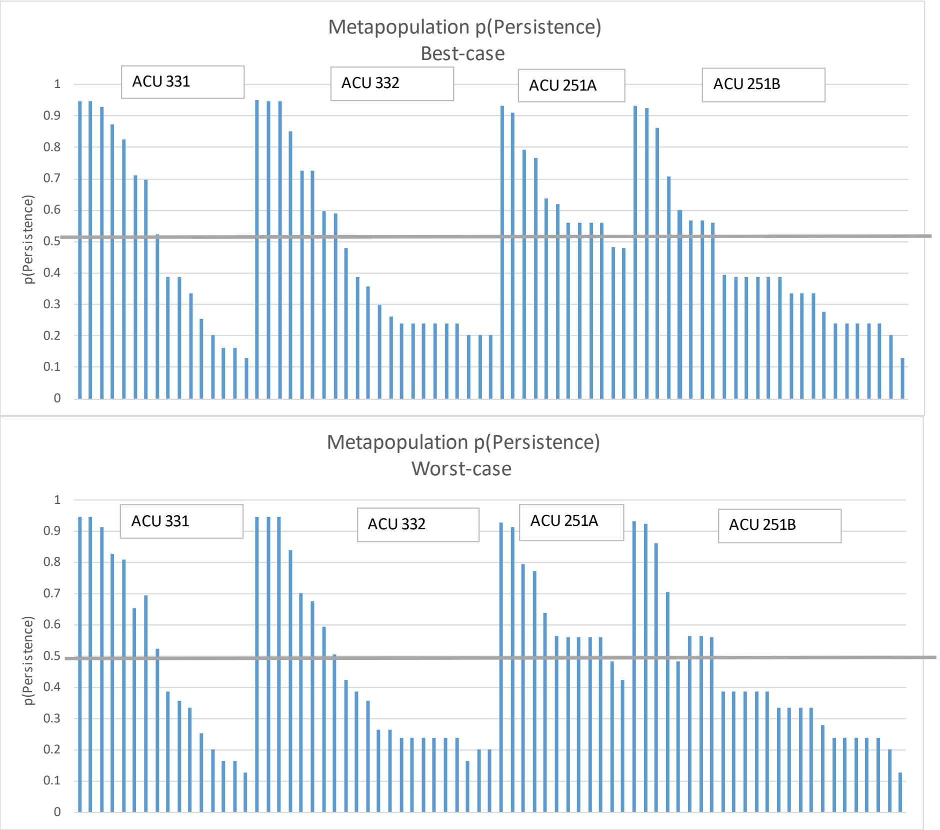


Figure 6.5. The predicted probability of persistence in 20 years for metapopulations comprising the each ACU under the best and worst-case scenarios

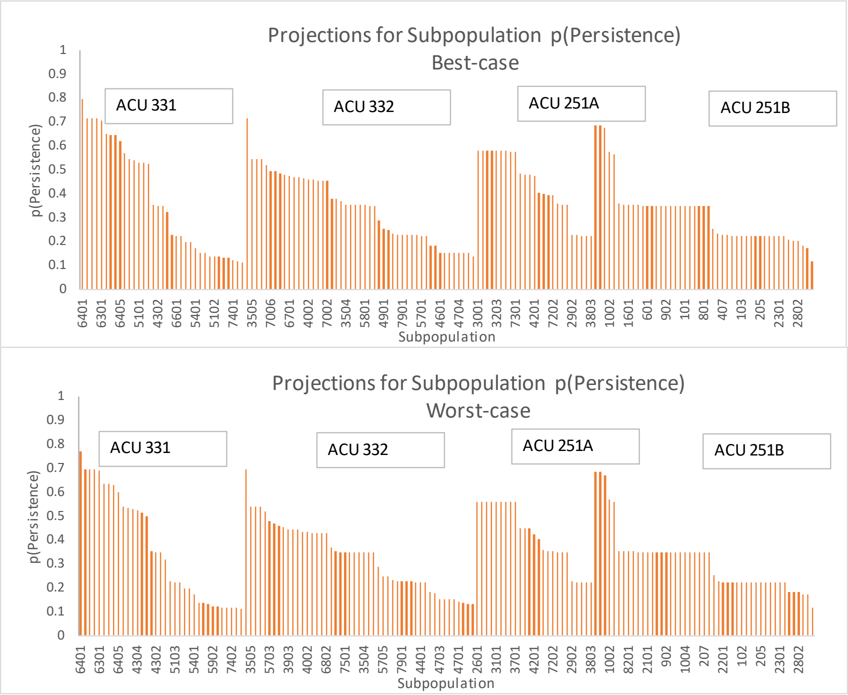


Figure 6.6. The predicted probability of persistence in 20 years for all extant and unknown subpopulations under the best and worst-case scenarios

Chapter 7. Synthesis

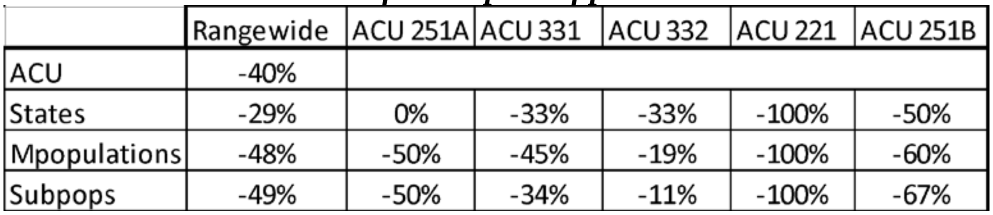
This Chapter synthesizes the results from our historical, current, and future analyses and discusses the consequences for the future viability of Dakota skipper. We assessed the viability of Dakota skipper by evaluating the ability of the species to maintain a sufficient number and distribution of healthy populations to withstand environmental stochasticity (resiliency), catastrophes (redundancy), and novel changes in its environment (representation).

7.1 Trend in the number, health, and distribution of populations

Rangewide Trend

The Dakota skipper occurred historically across a broad part of the Upper Midwest before much of the region’s prairie was destroyed, beginning in the 1800s. Declines in populations have occurred, with 48% of the metapopulations and 49% of the subpopulations extirpated to date (Table 7.1). The species is now likely extirpated from two states and one entire ACU, the Broadleaved Forests, Continental Province (ACU 221) (see Table 7.1).[4] Reasons the for the decline include: (1) a reduction in the extent of habitat; (2) fragmentation and isolation of the remaining habitat patches; and, (3) stress on the remaining populations caused by invasive species and incompatible land management practices, including neglect. These factors have allowed habitat conditions to deteriorate, have resulted in unsustainably high levels of mortality, or both. The health of the remaining extant populations is low, with 56% of the populations having less than a 50% chance of persisting in 10 years under present conditions (Figure 7.1).

Table 7.1. The percent loss of ACU, States/Provinces, and populations to date. Note, the losses are likely significant underestimates because the vast majority of surveys for the species were conducted well after the peak of prairie conversion



	Rangewide	ACU 251A	ACU 331	ACU 332	ACU 221	ACU 251B
ACU	-40%					
States	-29%	0%	-33%	-33%	-100%	-50%
Mpopulations	-48%	-50%	-45%	-19%	-100%	-60%
Subpops	-49%	-50%	-34%	-11%	-100%	-67%

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[4] The extent of its former abundance and distribution in ACU 221 and in the southern and eastern parts of ACU 251B is uncertain due to the general lack of survey effort before the 1960s. Only nine (3%) of the 306 site records for the species were collected before 1965. As destruction of the prairie in the Midwest began in about 1830 (Samson and Knopf 1994, p. 418), it is likely that extirpations in portions of the species’ range are undocumented.

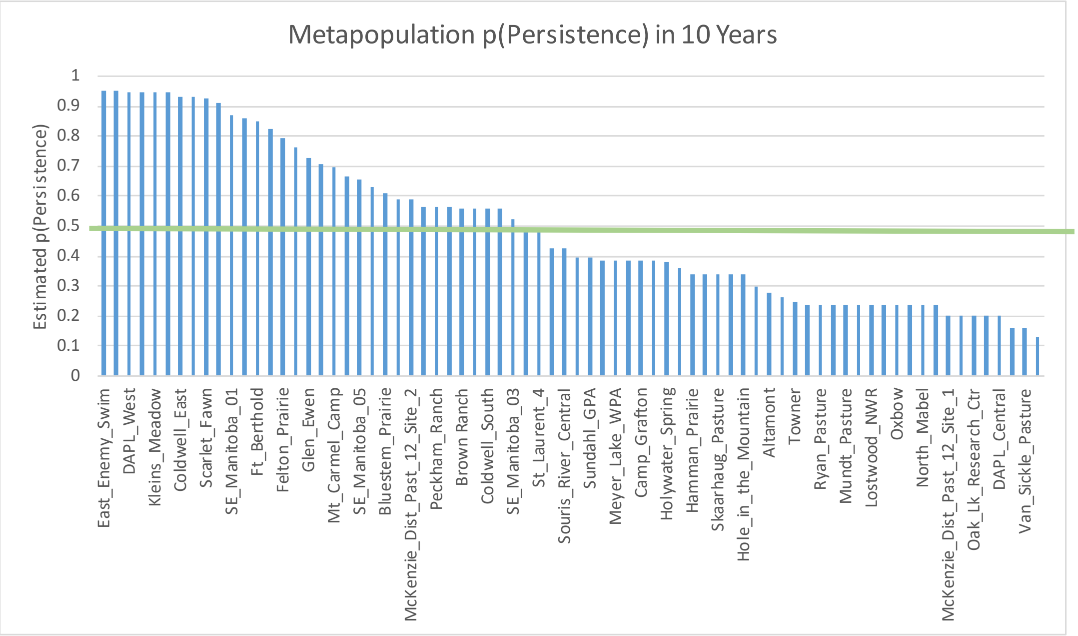

Figure 7.1. Projections for metapopulation persistence over the next 10 years under present-state conditions. A line at probability of persistence of 0.5 is provided as a visual reference

Under future state conditions, the health of the populations is not expected to markedly change from its current trend. Although for 13% of metapopulations, the predicted probability of persistence is greater than 0.90, for more than half of the metapopulations, the probability of persistence is less than 0.50 (Table 7.2). Of the 75 metapopulations, the predicted probabilities of persistence increase for 16 and decrease for 2 under the best-case scenario, and 11 increase and 17 decrease under the worst-case scenario (Figure 7.2a); for the majority of populations, the predicted probabilities remain unchanged (Figure 7.2b). Additionally, based on climate modeling, the future conditions may be exacerbated by anticipated changes. Under the 8.5 emissions scenario, for example, there is forecasted increase in annual precipitation and extended spring and fall seasons, which may lead to loss or degradation of prairie habitats (especially in Type A habitats). Thus, Dakota skipper future projections 20 years and beyond could be worse than predicted by our analyses.

Table 7.2. The percent of metapopulations that have probability of persistence: a) less than 0.20, b)0.50, and c) greater than 0.90

	Current	Best case	Worst case
pP < 0.20	12%	5%	7%
pP < 0.50	56%	55%	56%
pP > 0.90	13%	13%	13%

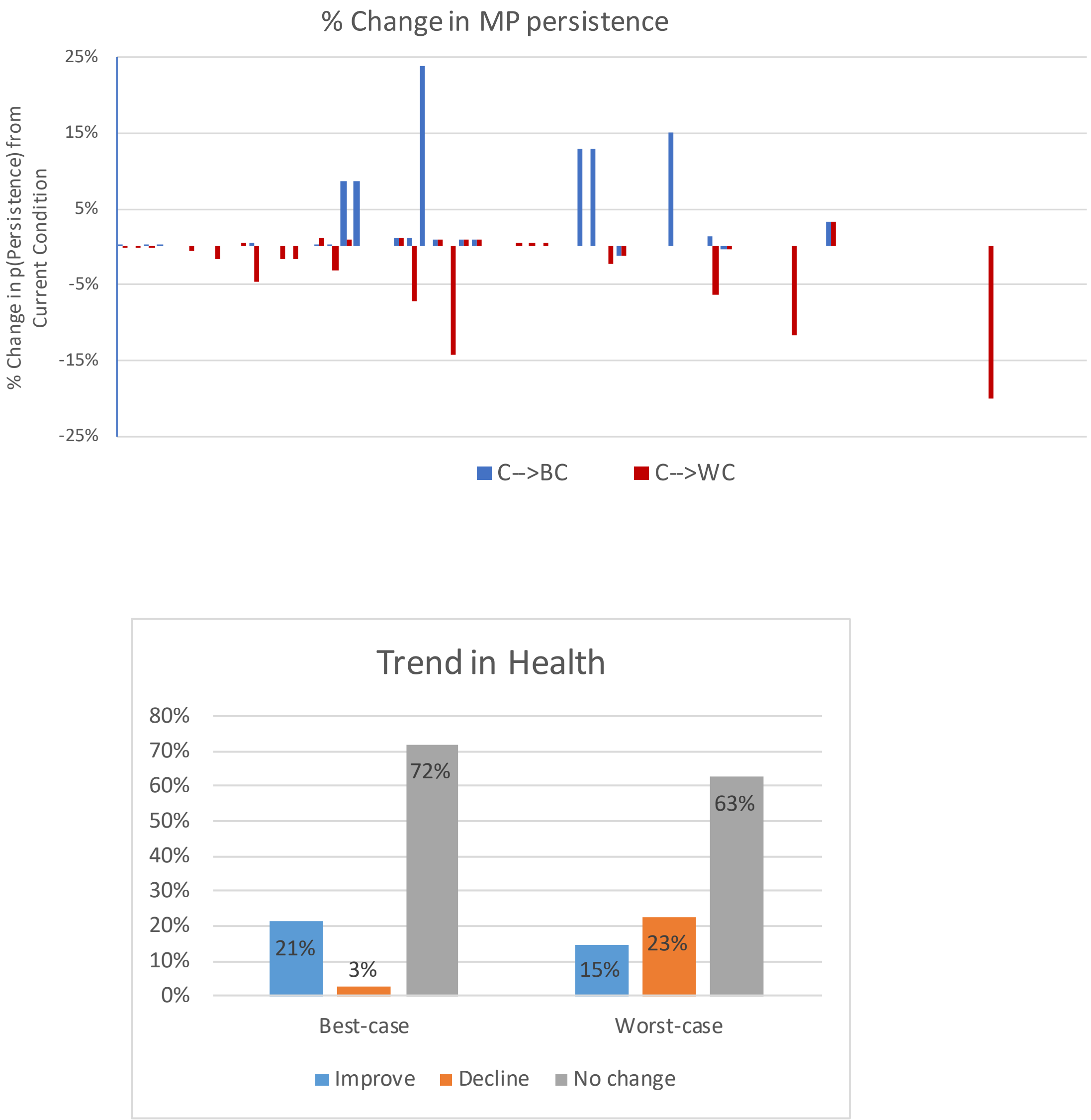

Figure 7.2. a) Percent change in the estimates of probability of persistence from current to 20 years into the future under the best-case (blue) and worst-case (red) scenarios. b) Percent of metapopulations projected to improve, decline, and remain unchanged under the best-case and worst-case scenarios.

Adaptive Capacity Unit Trends

The relative proportion of extirpated Dakota skipper metapopulations to date varies geographically, with trends worsening generally from east to west (see Table 7.1 and Figure 1.5). As stated above, very few populations were recorded in the easternmost ACU (221)--a region of massive and early conversion of prairie--and the species is now likely extirpated there.

The next greatest decline has occurred in ACU 251B; an area that represented 43% of the historical range (Figure 7.3). Currently, 60% of its metapopulations and 67% of its subpopulations are extirpated (Table 7.1). The health of the remaining extant populations varies, with probability of persistence ranging from 0.13 to 0.93 (Table 7.3). The distribution, however, is skewed towards the lower end (Figure 7.4); only 2 metapopulations have a probability of persistence greater than 0.9, and more than half of the metapopulations having less than a 50% chance of persisting (Table 7.3). Historically, Dakota skipper occurred in 63 metapopulations made up of 143 subpopulations and covered a large portion of the northern end of ACU 251B. Today, there are only 25 metapopulations consisting of 47 subpopulations, with populations restricted to the northwest corner of the ACU and only one site in Minnesota which was a reintroduction of an extirpated site.

In ACU 251A, 50% of its metapopulations and subpopulations are extirpated (Table 7.1). The health of the remaining extant populations is similar to ACU 251B in that only 2 populations have probability of persistence greater than 0.9 (Table 7.3) but differs in that the health of most populations lies between 0.50 and 0.90 (Figure 7.4). ACU 251A has about half of the populations of ACU 251B, but on average, its populations have higher chances of persistence (an average of 66% in ACU 251A vs 43% in ACU 251B, Table 7.3). Although there is no change in the number of states occupied, there has been a noticeable loss of occupancy. Historically, Dakota skipper occurred in 24 metapopulations made up of 50 subpopulations and with populations distributed throughout most of ACU 251A. Today, there are 12 metapopulations consisting of 25 subpopulations. The western and southernmost populations are extirpated, as well as, a substantial number of sites between northern Manitoba and northwest Minnesota, which are now separated by over 375 kilometers (233 miles).

In ACU 331, 45% of its metapopulations and 34% of its subpopulations have been extirpated. The health of the remaining populations is similar to ACUs 251A and 251B with only three populations having estimated probability of persistence greater than 0.9 and half have less than a 50% chance of persisting (Table 7.3). The metapopulations with good health occur in clusters; two in a southwestern Manitoba and one in north-central North Dakota, all of which are managed primarily with annual fall or late summer haying. The spatial extent of occupied areas in ACU 331 has not changed significantly but with the loss of 19 metapopulations and 24 subpopulations (Table 7.1), the distance between extant populations is increasing.

In ACU 332, 19% of its metapopulation and 11% of its subpopulations have been extirpated (Table 7.1). The health of the remaining populations is similar to ACU 251B; the range in persistence estimates is 0.13 to 0.93, but the distribution is skewed towards lower persistence (Figure 7.4). Only 3 populations having estimated probability of persistence greater than 0.9, while 64% having less than 0.50 probability of persisting (Table 7.3). The metapopulations with better health in this ACU occur in southeast Saskatchewan and north-west North Dakota, and Dakota skipper habitats are predominantly grazed. The spatial extent of the core occupied area of ACU 332 has not changed significantly but the isolated metapopulations in the southeast end of the ACU have been extirpated. This ACU, however, has the most potential for discovery of undocumented populations as the majority of subpopulations in this ACU, 33 of 37, were first discovered in 2014 or later. Although the overall health of the ACU could improve with new populations discovered, the loss of populations that has occurred indicates declining health of the ACU (just perhaps not a badly relative to the other ACUs as we currently believe).

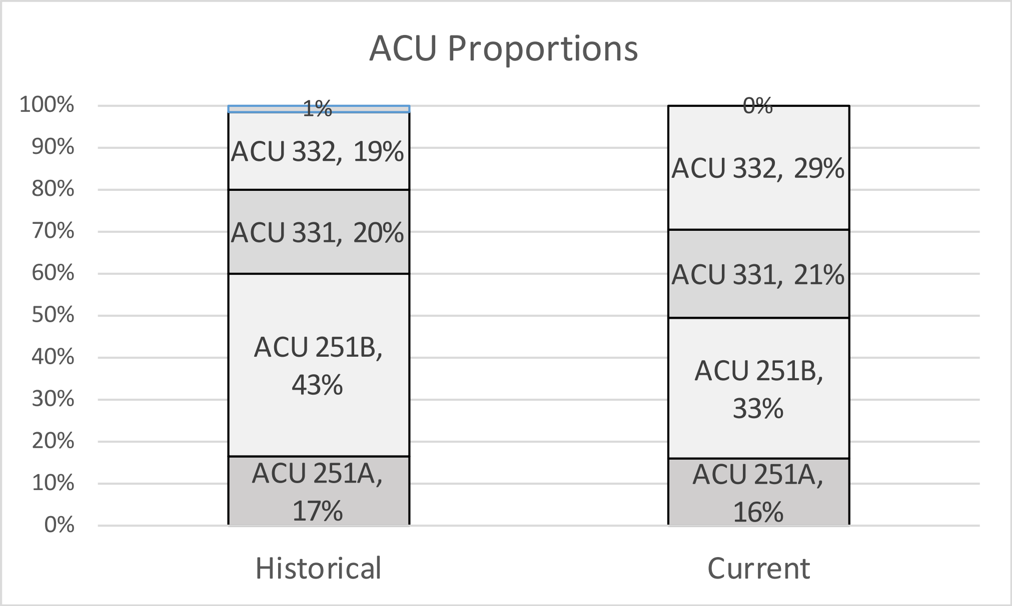

Figure 7.3. The proportion of metapopulations comprising each ACU over time

Table 7.4. The numerical distribution of metapopulations within the ACUs. The percent and number of extant metapopulations within each ACU: a) comprising the ACU, b) with projected p(persistence) values < 0.50, and c) with projected p(persistence) values > 0.90.

	ACU 251A		**ACU 331**		**ACU 332**		**ACU 251B**	
	%	**#**	**%**	**#**	**%**	**#**	**%**	**#**
Metapops	16%	12	21%	16	29%	22	33%	25
pP<0.50	17%	2	50%	8	64%	14	68%	17
pP>0.90	17%	2	19%	3	14%	3	8%	2
min pP	0.479	--	0.128	--	0.204	--	0.128	--
max pP	0.933	--	0.948	--	0.950	--	0.932	--
average pP	0.655	--	0.530	--	0.462	--	0.435	--

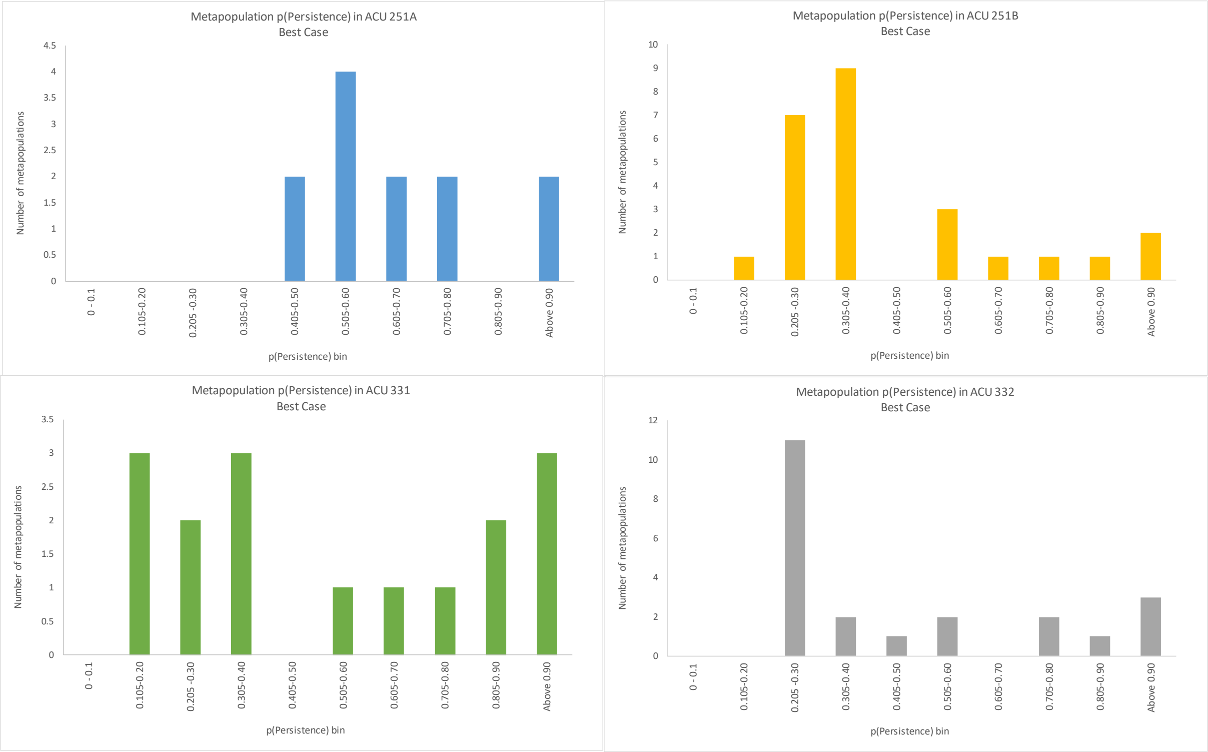

Figure 7.4. The distribution of metapopulations within ACUs by probability of persistence under the best-case scenario.

7.2. Implications for Viability

Resiliency

Dakota skipper resiliency is defined by the ability of populations to persist despite environmental stochasticity and transient disturbances and primarily relies upon the health of its populations, quality of the habitats inhabited by the species, and distribution of populations across heterogeneous conditions. The health of Dakota skipper populations has declined markedly over time due to: (1) a reduction in the extent of habitat; (2) fragmentation and isolation of the remaining habitat patches; and, (3) stress on the remaining populations caused by invasive species and incompatible land management practices, including neglect. These factors have allowed habitat conditions to deteriorate, have resulted in mortality that is unsustainable, and have minimized the likelihood that vacant habitat patches will be recolonized. Now the species is threatened by continued extirpation of sub- and metapopulations due to both stressors and stochastic factors. Given the present state conditions, only 42% of the remaining populations have a probability of persistence of greater than 0.5 and 14% have a probability of persistence greater than 0.90.

Dakota skipper habitat was once widespread and as a result, populations likely ebbed and flowed across the landscape in response to transient factors. These factors may have included locally intense grazing by bison, fire, cool springs, hot and dry summers, and flooding. The species was likely resilient to these factors due to: 1) its abundance and pervasiveness in habitats around areas where it was temporarily eliminated; 2) the ability of plant species important to the Dakota skipper to rebound soon after intense disturbances; 3) heterogeneous habitats that provided refugia from unfavorable weather conditions and some disturbances; and the broad distribution of populations east to west and south to north, likely fostered population synchrony.

The distribution of Dakota skipper populations is important to the species resiliency as well. As explained in Chapter 1, environmental stochasticity can act at a regional scale as well as locally, causing populations to fluctuate in synchrony over broad geographical areas (Hanski 1999, p. 372), which can lead to contemporaneous population losses across broad areas. Thus, populations distributed across a diversity of environmental conditions help guard against concurrent losses of populations by inducing asynchronous fluctuations among populations. Rangewide, there has been a 25% loss in the number of sections/ecoregions once occupied by Dakota skipper, with the greatest number of losses occurring in ACU 251B (Table 7.3).

Table 7.3. The number of Sections/Ecoregions occupied historically and currently.

	Historical	**Current**	**% loss**
Rangewide	12	9	-25%
ACU 251A	3	2	-33%
ACU 331	3	3	0%
ACU 332	3	3	0%
ACU 221	1	0	-100%
ACU 251B	2	1	-50%

In ACU 251A, the species is extirpated from one of the three Sections/Ecoregions (U.S./Canada) in which it occurred historically – the Interlake Plain (Canada) (Tables 3.3 and 4.2). This has reduced the resiliency of the species within this ACU to the extent that the species occurrence and distribution in these two areas provided a buffer against declines elsewhere in the ACU. This lost resiliency may be large in light of the geographic extent of the two remaining geographic areas. The Red River Valley Section has retained only two of the 18 metapopulations recorded in this ACU. Conservation of the species in this section may have high importance for maintaining resiliency within this ACU. The Lake Manitoba Plain contains 9 extant metapopulations and only two that are known to have been extirpated.

In ACU 251B, the species is extirpated from one of the two Ecoregion Sections in which it occurred historically – the Central Dissected Till Plains Section (U.S.) (Tables 3.3 and 4.2). About 63% of the metapopulations in the North-Central Glaciated Plains Section have been extirpated, but 25 remain extant.

In ACUs 331 and 332, all historical Sections/Ecoregions remain occupied. In ACU 331, despite over half of the recorded metapopulations are extirpated from Northeastern Glaciated Plains Section (Tables 3.3 and 4.2), 13 metapopulations persist thereby providing opportunity to maintain the species in this geographic area. In ACU 332, the species maintains a somewhat balanced distribution between the two sections that it inhabits – the Northern Glaciated Plains Section and the Northwestern Great Plains Section (Tables 3.4 and 4.2).

Given the Dakota skipper phenology varies by latitude, maintaining populations in the both the northern and southern portions of the range is likely the most influential factor in preserving population asynchrony (R. Dana, pers. comm. 2018). Given that the species has been extirpated from southern portion of its range (Figure 7.3), it is therefore likely that species' inherent ability for ensuring population asynchrony has been diminished.

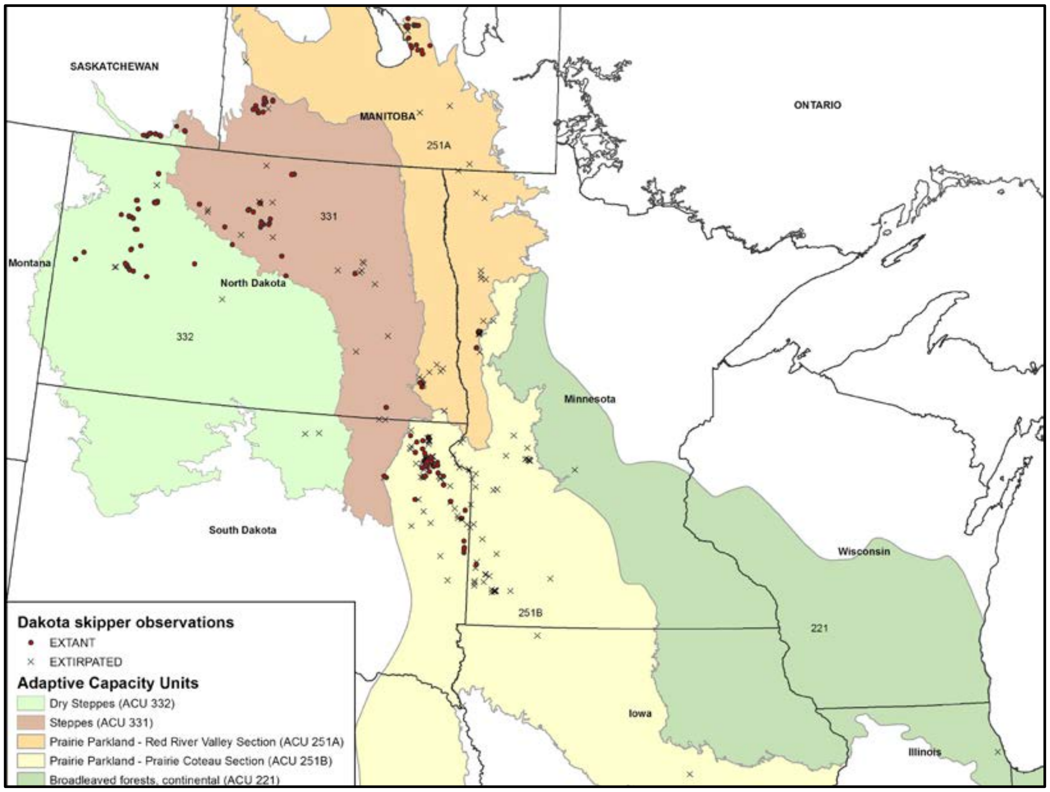

Figure 7.3. The current distribution of Dakota skipper. Red circles represent Dakota skipper sites where presence is extant or unknown, black X's represent sites where the species is no longer present.

Additionally, resiliency also requires connectivity among populations for gene flow and demographic rescue. Today, however, many populations are fragmented and isolated, with 73% of the metapopulations having 2 or fewer subpopulations (Figure 7.4). More than half (57%) of the metapopulations consist of only one subpopulation and likely have almost no chance of recovery from a local extirpation. Their persistence, therefore, is dependent on the implementation of compatible land management and the mitigation of other stressors. Some land managers and landowners are trying to design and implement practices that are compatible with healthy populations of the Dakota skipper. These efforts will have to be extensive to arrest the species' continued decline, however.

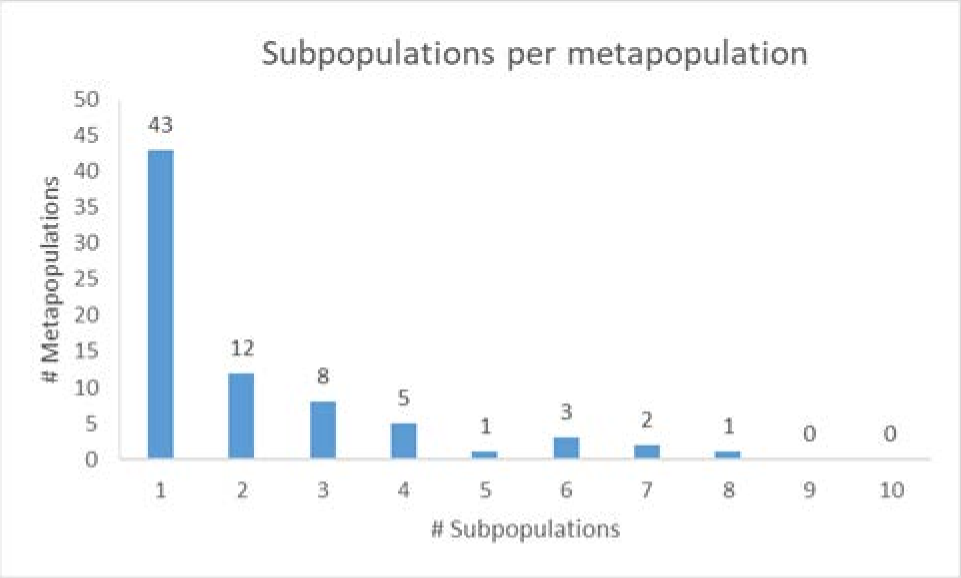

Figure 7.4. The current number of subpopulations comprising the metapopulations

Redundancy

Dakota skipper redundancy is influenced primarily by the distribution of populations across spatially heterogeneous environments that would allow the species to persist in the event of a large scale drought. We do not know how many populations of the Dakota skipper occurred historically, but we may infer from the geographic dispersion of the species' records coupled with available genetic information (Britten and Glasford 2002) that populations were widespread and contiguous over broad areas. The spatial dispersion of the species likely contributed to its persistence in the face of extreme and widespread drought, like that which occurred in the 1930s.

Current redundancy of the Dakota skipper is reduced greatly compared to historical conditions, due to wide scale habitat destruction and other factors that have isolated and extirpated populations. Conversion of prairie for agriculture and urbanization completely eliminated the species from broad geographic areas that comprised the eastern and southern portions of its range, including one entire ACU. Additional habitat conversion, incompatible management practices, and other stressors have further eroded the species redundancy by reducing the number of populations and the geographic area inhabited by the species.

Despite the marked reduction in the Dakota skipper's historical abundance and distribution, the species' viability benefits today from the variety of ecological settings in which it has survived and the geographic extent of its distribution. The frequency and intensity of droughts likely vary across the many different ecological settings and landscapes that the species still inhabits. Thus, it seems that the species' current widespread distribution provides some buffer against rangewide-scale catastrophic drought. Similarly, the broad distribution likely provides buffer against rangewide-scale pesticide applications events. We have not yet, however, quantitatively assessed the past, current, and future vulnerability of Dakota skipper populations to these types of catastrophes. Nor have we fully assessed the implications of climate change.

Representation

Dakota skipper representation is influenced by the breadth of adaptive diversity possessed by Dakota skipper and by maintaining the evolutionary processes (i.e., gene flow and natural selection) that drive adaptation. Assuming the delineated ACUs represent unique sources of adaptive diversity, Dakota skipper may have reduced ability to adapt to novel changes (e.g., diseases, predators, climate, etc.) in its environment. The complete loss of the species from broad areas in the southern and easternmost portion of the species range--from ACU 221 and from the south and eastern part of ACU 251B--suggests that a substantial amount of the Dakota skipper's adaptive capacity has already been lost. The isolation of the species into fragments of its historical habitat may have further eroded adaptive capacity that developed at smaller scales within ACUs. More importantly, the current fragmented landscape has greatly impeded gene flow between populations and thereby impairing adaptation.

Looking into the future, further losses of adaptive diversity seem likely given the low health of the majority of metapopulations. In addition to the likely continued loss of populations within ACUs and any corresponding loss of unique adaptations occurring at this scale, ACU-wide extirpation is possible thereby leading to broad-scale losses in adaptive capacity. Furthermore, the loss of connectivity among populations has likely greatly diminished gene flow among populations, which will impede process of evolution. Restoring gene flow and ensuring populations experience varying selection pressures (by ensuring populations persist in a diversity of ecological settings) is needed to maintain the processes that allow adaptation to occur.

Synopsis

The number, health, and distribution of Dakota skipper populations have declined over time and are projected to continue to decline into the future. With these losses, the ability of the species to withstand normal environmental variation, catastrophes, and its ability to adapt to novel changes such as diseases and climate has been greatly diminished. The extent to which its capacity to withstand and adapt to these changes is unknown, but the magnitude of decline that has occurred has increased the species' vulnerability to extinction.

To improve Dakota skipper viability, it is necessary to:

1. Increase resiliency by:
    a. improving the health of populations by increasing population size of metapopulations through enhancement of floral species diversity within existing prairies
    a. restoring connectivity within and among populations to improve gene flow
    b. ensuring population asynchrony within ACUs by maintaining and restoring populations over a diversity of habitats and environmental conditions
    c. ensuring disturbance processes occur outside the peak flight period, preferably after the flight period and minimizing impacts during larval development.
2. Increase redundancy by restoring and protecting multiple populations in areas with low risk of drought, and ensuring these populations are sufficiently dispersed to minimize the risk of all populations within an ACU being exposed simultaneously to catastrophic drought conditions

3. Increase representation by improving resiliency and redundancy within each of the ACUs and by restoring gene flow between populations.

7.3 Key Uncertainties

Inherently, predicting the future condition requires us to make plausible assumptions. Our analyses are predicated on multiple assumptions, which could lead to over- and underestimates of viability. Below we identify the key sources of uncertainty.

Status and Abundance of Populations

For many populations (n=87), we had insufficient data to conclusively determine whether the population was extant or extirpated, and for most populations we have limited information about local conditions. Thus, the predictions for subpopulation, and hence metapopulation, persistence are predicated assumptions about status, abundance, and habitat conditions. These uncertainties minimize our ability to characterize the health of subpopulations and metapopulations and the stressors to which they are exposed accurately and reliably, thus, affect our ability to plan and implement actions that will contribute to population health.

Spatial Variation in Adaptive Diversity

It is unclear which populations, if any, may be especially important for the preservation of the species' adaptive capability. Based on evolutionary principles, it is likely that each of the identified ACUs provide unique conditions in which populations must be adapted to. Whether specific populations within ACUs may hold particular importance for the conservation of the species' remaining adaptive capacity may warrant further analysis in recovery planning efforts for the species. Each ACU, for example, could be further subdivided to distinguish additional environmental diversity. Sections and Subsections are subregions of Bailey's ecosystem provinces that are based on differences in environmental and biological features and landforms (Bailey 1998; 2004). These distinct sets of features and landforms may be indicative of additional genetic and environmental diversity that warrant preservation to ensure that the Dakota skipper may adapt to future changes to its environment. Sections and Subsections of the ecosystem provinces (ACUs) have not been developed for Canada. We could use a unit called "ecoregions" that was developed for Canada by the Ecological Stratification Working Group and is similar in scale to Bailey's sections (1995).

General Life History

Much is still unknown about the general life history characteristics of the Dakota skipper; especially the larval life stage. Dakota skippers spend the majority of their life in the larval stage, however because they are extremely difficult to locate in their larval habitats, limited information has been recorded. Overall, we still have poor understanding of the structure and function of populations, including the drivers of inter- and intra-population dynamics. Finally, more quantitative data are needed on specific habitat requirements of both immature and adults stages. To expound on that, information is lacking on dispersal habitat requirements and how that affects dispersal ability (and distance), as well as population viability in reconstructed prairies (reconstructing native prairie forbs and grasses on previously-cropped land).

Grazing Management

There are nuances that must be considered when planning and implementing management to ensure the health of Dakota skipper populations. Grazing, however, may hold the most uncertainty in terms of how to ensure that grazing is carried out in a manner that is compatible with Dakota skipper conservation. In light of the large number of populations subject to grazing management, these uncertainties need to be better understood and alleviated through a partnership that includes biologists, range ecologists, and ranchers.

Other Key Uncertainties

Other key uncertainties were identified by the SSA team including susceptibility to pesticides, primarily insecticides, drought, changes in hydrologic cycles, direct and indirect effects of climate change; and mortality due to natural enemies. All of these could have wide-ranging effects if populations are susceptible.

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Appendix 1. Estimated Metapopulation Probability of Persistence results from BBN model for the current time-period and 10-year best and worst-case scenarios.

ACU	MP #	Metapopulation Name	Current pP	Best pP	Worst pP
285	1	East_Enemy_Swim	0.9230	0.9230	0.9230
285	2	Bitter_Lake	0.7067	0.7067	0.7067
285	4	Oak_Island_Wike_WPA	0.8610	0.8610	0.8610
304	6	Peckham_Ranch	0.5615	0.5666	0.5666
285	7	Blue_Dog_Lake	0.1278	0.1278	0.1278
296	8	Hamman_Prairie	0.3368	0.3368	0.3368
304	9	Whipple_Ranch	0.5615	0.5666	0.5666
285	10	Scarlet_Fawn	0.9255	0.9255	0.9255
304	11	Berwald_Schuchard_WPA	0.3875	0.3875	0.3875
304	13	Meyer_Lake_WPA	0.3875	0.3875	0.3875
296	15	Roy_West_GPA	0.2397	0.2397	0.2397
296	16	North_Red_Iron_Lake_WPA	0.3875	0.3875	0.3875
296	19	Ryan_Pasture	0.2397	0.2397	0.2397
296	20	Black_Slough_GPA	0.3368	0.3368	0.3368
304	21	Skaarhaug_Pasture	0.3368	0.3875	0.3368
296	22	S_Buffalo_Lk	0.2397	0.2397	0.2397
296	23	Mundt_Pasture	0.2397	0.2397	0.2397
304	24	Sundahl_GPA	0.3935	0.3887	0.3887
285	26	Armstrong	0.5594	0.5594	0.5620
285	27	Bluestem_Prairie	0.6110	0.6183	0.5666
285	28	Brookings_Co_Pastures	0.4847	0.6005	0.4847
285	29	Brown Ranch	0.5595	0.5595	0.5595
285	30	Coldwell_East	0.9325	0.9325	0.9281

ACU	**MP #**	**Metapopulation Name**	**Current pP**	**Best pP**	**Worst pP**
304	31	Coldwell_South	0.5594	0.5594	0.5620
285	32	Coldwell_West	0.9084	0.9084	0.9136
304	33	Crystal_Springs_Preserve	0.5620	0.5620	0.5620
296	34	DAPL_East	0.2397	0.2397	0.2397
285	35	DAPL_West	0.9483	0.9483	0.9468
296	36	Eagle_Nest_Butte	0.3579	0.3565	0.3565
296	37	Eriksdale	0.5594	0.5594	0.5620
285	38	Felton_Prairie	0.7928	0.7928	0.7928
285	39	Ft_Berthold	0.8514	0.8514	0.8373
285	40	Glen_Ewen	0.7260	0.7267	0.7034
285	41	Holywater_Spring	0.3803	0.3855	0.3565
296	42	IL50	0.4242	0.4794	0.4242
285	43	Kleins_Meadow	0.9478	0.9480	0.9478
296	44	Lostwood_NWR	0.2397	0.2397	0.2397
285	45	Martin_Site	0.1278	0.1278	0.1278
304	46	McKenzie_Dist_Past_12_Site_1	0.2035	0.2035	0.1629
285	47	McKenzie_Dist_Past_12_Site_2	0.5885	0.5885	0.5049
296	48	McKenzie_Dist_Past_6	0.2397	0.2397	0.2397
296	49	Minnkota_Power_Site	0.2984	0.2984	0.2637
296	50	Mountrail_Co_Site_2016	0.2637	0.2637	0.2637
285	51	Mt_Carmel_Camp	0.6958	0.6958	0.6958
304	52	New_Frontier	0.2035	0.2035	0.2035
304	53	Oak_Lk_Research_Ctr	0.2035	0.2035	0.2035
296	54	Oakes	0.2035	0.2035	0.2035
285	55	Oxbow	0.2397	0.2397	0.2397

ACU	MP #	Metapopulation Name	Current pP	Best pP	Worst pP
285	56	Sandpiper_Berthold	0.1629	0.1629	0.1629
285	57	Sandpiper_Mountrail_Co_East	0.9462	0.9462	0.9462
285	58	Sandpiper_Mountrail_Co_West	0.5902	0.5954	0.5954
285	59	SE_Manitoba_01	0.8677	0.8729	0.8270
304	60	SE_Manitoba_02	0.3368	0.3368	0.3368
296	61	SE_Manitoba_03	0.5236	0.5236	0.5236
285	63	SE_Manitoba_05	0.6545	0.7115	0.6545
296	64	SE_Manitoba_06	0.9480	0.9483	0.9462
285	65	SE_Manitoba_07	0.9284	0.9284	0.9124
285	66	Smokey_Lake	0.8246	0.8246	0.8109
296	67	Souris_River_Central	0.4242	0.4794	0.4242
285	68	Souris_River_East_01	0.6678	0.7260	0.6746
296	69	Camp_Grafton	0.3875	0.3875	0.3875
285	70	Souris_River_West	0.9495	0.9496	0.9482
285	71	St_Laurent_4	0.4835	0.4835	0.4835
296	72	St_Laurent_East	0.6308	0.6378	0.6378
285	73	St_Laurent_West	0.7650	0.7662	0.7731
296	74	Towner	0.2464	0.2546	0.2546
296	75	McKenzie_Krych_observation	0.3875	0.3875	0.3875
304	76	DAPL_Central	0.2035	0.2035	0.2035
285	77	Garrison_Training_Area	0.2397	0.2397	0.2397
285	78	Van_Sickle_Pasture	0.1629	0.1629	0.1629
285	79	North_Mabel	0.2397	0.2397	0.2397
296	81	Altamont	0.2782	0.2782	0.2782
296	82	Sica_Hollow	0.3963	0.3963	0.3875

ACU	MP #	Metapopulation Name	Current pP	Best pP	Worst pP
296	83	Yellow_Bank	0.2397	0.2397	0.2397
304	84	Hole_in_the_Mountain	0.3368	0.3368	0.3368

Appendix 2. Estimated Subpopulation Probability of Persistence results from BBN model for the current time-period and 10-year best and worst-case scenarios.

ACU	Subpop #	Subpopulation Name	pP-Current	pP - Best	pP - Worst
285	101	Albrecht Pasture	0.3479	0.3482	0.3476
285	102	Blocks Pasture	0.2255	0.2260	0.2251
285	103	Chekapa Creek Ridge	0.2255	0.2253	0.2255
285	104	East Enemy Swim Lake Prairie	0.6866	0.6870	0.6864
285	105	Gollnick Hay Prairie	0.3479	0.3483	0.3477
285	107	Lewandowski Hay Prairie	0.3478	0.3481	0.3476
285	111	North Enemy Swim Lake Prairie	0.6866	0.6870	0.6866
285	203	East Bitter Lake	0.2245	0.2246	0.2245
285	205	East Hinkleman Bitter Lk Pasture North	0.2245	0.2246	0.2245
285	206	Narem Pasture	0.2246	0.2247	0.2247
285	207	Southeast Bitter Lake	0.3476	0.3479	0.3474
285	402	Fisher Hay Prairie	0.3493	0.3499	0.3487
285	403	Goodboy Prairie	0.2245	0.2246	0.2246
285	406	North Owl Lake Prairie	0.2244	0.2245	0.2244
285	407	Oak Island Prairie	0.2257	0.2261	0.2253
285	408	Wike Hay Prairie	0.2243	0.2244	0.2244
285	409	Wike WPA	0.3539	0.3544	0.3539

ACU	Subpop #	Subpopulation Name	pP- Current	pP - Best	pP - Worst
296	601	Peckham Ranch	0.3493	0.3499	0.3497
296	602	Townsends	0.3479	0.3482	0.3482
285	702	North Blue Dog Lake	0.1180	0.1182	0.1179
285	801	Hamman Prairie	0.3471	0.3478	0.3470
285	901	Whipple Ranch G1/G2	0.3483	0.3486	0.3479
285	902	Whipple Ranch G16	0.3482	0.3485	0.3479
285	1001	Anderson Pasture	0.3480	0.3483	0.3477
285	1002	Hayes Prairie	0.5731	0.5761	0.5700
285	1003	Scarlet Fawn Prairie	0.6742	0.6754	0.6724
285	1004	Tetankamoni Prairie	0.3480	0.3483	0.3476
285	1101	Berwald/Schuchard WPA	0.3561	0.3561	0.3560
285	1301	Meyer Lake WPA	0.3511	0.3521	0.3503
285	1501	Roy West GPA	0.2300	0.2328	0.2280
285	1601	North Red Iron Lake WPA	0.3540	0.3555	0.3521
285	1901	Ryan Pasture	0.2244	0.2245	0.2244
285	2001	Black Slough GPA	0.3482	0.3487	0.3477
285	2101	Skaarhaug Pasture	0.3496	0.3503	0.3488
285	2201	South Buffalo Lake	0.2255	0.2253	0.2256
285	2301	Mundt Pasture	0.2244	0.2245	0.2244
285	2401	Sundahl GPA	0.2252	0.2255	0.2243
285	2402	Abbey of the Hills Prairie	0.1845	0.1853	0.1746
285	2601	Armstrong	0.5751	0.5759	0.5623
285	2701	Bluestem Prairie	0.3513	0.3529	0.3479
285	2702	Buffalo R SP	0.3509	0.3536	0.3481

ACU	Subpop #	Subpopulation Name	pP-Current	pP - Best	pP - Worst
285	2801	Buffalo Ridge II Wind Power Project	0.1882	0.2005	0.1825
285	2802	Brookings Co Private Pasture	0.1882	0.2005	0.1825
285	2803	Buffalo Ridge II Wind Power Project_Sites_3-6	0.1882	0.2099	0.1825
296	2901	Gregor	0.2248	0.2247	0.2248
296	2902	Milton Sr.	0.2267	0.2282	0.2267
296	2903	Schultz	0.2252	0.2273	0.2252
285	3001	Coldwell 1	0.5768	0.5777	0.5612
285	3002	Coldwell 2	0.4828	0.4847	0.4483
285	3003	Coldwell 3	0.5768	0.5777	0.5612
285	3004	Coldwell 4	0.3945	0.3969	0.3479
285	3101	Coldwell 5	0.5768	0.5777	0.5612
285	3202	Coldwell 7	0.5768	0.5777	0.5612
285	3203	Coldwell 9	0.5768	0.5777	0.5612
285	3204	Coldwell 10	0.5768	0.5777	0.5612
285	3301	Crystal Springs Preserve	0.5637	0.5652	0.5607
304	3401	DAPL 9	0.2259	0.2259	0.2259
304	3501	DAPL 1	0.5436	0.5452	0.5410
304	3502	DAPL 2	0.3512	0.3535	0.3487
304	3503	DAPL 3	0.3519	0.3545	0.3492
304	3504	DAPL 4	0.3524	0.3555	0.3491
304	3505	DAPL 5	0.5437	0.5455	0.5412
304	3506	DAPL 6	0.5433	0.5449	0.5408
304	3507	DAPL 7	0.3677	0.3799	0.3510
304	3601	Eagle Nest Butte	0.1524	0.1524	0.1524

ACU	Subpop #	Subpopulation Name	pP-Current	pP - Best	pP - Worst
304	3603	Eagle Nest Butte South	0.1524	0.1524	0.1524
285	3701	Eriksdale	0.5768	0.5777	0.5612
285	3801	Bicentennial Prairie	0.4015	0.4032	0.4032
285	3802	Blazing Star Prairie	0.3565	0.3565	0.3565
285	3803	Felton Prairie County Unit	0.2237	0.2237	0.2237
285	3804	B-Bar-B Ranch - Unit A	0.2244	0.2241	0.2255
304	3901	Marathon Oil - Nicholi	0.4680	0.4680	0.4680
304	3902	Marathon Oil - Amelia West	0.4726	0.4861	0.4592
304	3903	Marathon Oil - Amelia East	0.4514	0.4582	0.4445
296	4001	14km S. of Glen Ewen on E. slope of Souris River	0.4553	0.4636	0.4532
296	4002	2.1km S Hwy 18 & 601 near Glen Ewen	0.4507	0.4591	0.4349
296	4101	Holywater Spring East	0.1990	0.1992	0.1988
296	4102	Holywater Spring West	0.2001	0.2005	0.1994
285	4201	IL50	0.4449	0.4751	0.4262
296	4301	Cooperdahl Hill	0.1171	0.1307	0.1152
296	4302	Eidmann Ranch-East	0.3469	0.3469	0.3468
296	4303	Eidmann Ranch-West	0.3468	0.3468	0.3468
296	4304	Kleins Meadow	0.5274	0.5274	0.5259
296	4305	Swearsons Meadow	0.6399	0.6474	0.6377
296	4306	Swearsons School	0.6399	0.6474	0.6377
296	4401	Lostwood NWR	0.2250	0.2236	0.2250
296	4501	Martin Site	0.1148	0.1148	0.1148
304	4601	McKenzie District Pasture 12, Site 1	0.1532	0.1532	0.1349
304	4701	McKenzie District Pasture 12, Site 2	0.1532	0.1532	0.1419

ACU	Subpop #	Subpopulation Name	pP- Current	pP - Best	pP - Worst
304	4702	McKenzie District Pasture 12 - Site 2 North	0.1532	0.1532	0.1349
304	4703	Angus Charolaise Simmental Oil Pad - Unit 1	0.1532	0.1532	0.1532
304	4704	Angus Charolaise Simmental Oil Pad - Unit 2	0.1532	0.1532	0.1532
304	4801	McKenzie District Pasture 6	0.2304	0.2304	0.2304
296	4901	Minnkota Power Site	0.2529	0.2557	0.2471
304	5001	Mountrail County Site - 2016	0.2336	0.2336	0.2336
296	5101	Mt. Carmel Camp	0.5292	0.5292	0.5292
296	5102	Mt. Carmel Camp SW	0.1385	0.1385	0.1385
296	5103	Thompson Ranch	0.2243	0.2230	0.2251
296	5201	New Frontier	0.1810	0.1831	0.1778
285	5301	Oak Lk Research Ctr	0.1735	0.1748	0.1710
296	5401	Oakes	0.1708	0.1715	0.1706
296	5501	Oxbow	0.2263	0.2278	0.2251
296	5601	Sandpiper Pipeline GLHWA032a2_DS	0.1387	0.1387	0.1387
304	5701	Mountrail County Site	0.2244	0.2244	0.2244
304	5702	Sandpiper Pipeline GLHMO050a_DS	0.1372	0.1372	0.1372
304	5703	Sandpiper Pipeline GLHMO052b_DS	0.4803	0.4803	0.4803
304	5704	Sandpiper Pipeline GLHMO056.210a1_DS1	0.2869	0.2869	0.2869
304	5705	Sandpiper Pipeline GLHMO056.210a1_DS2	0.2506	0.2506	0.2506
304	5706	Sandpiper Pipeline GLHMO047a_DS1	0.5175	0.5175	0.5175
304	5707	Sandpiper Pipeline GLHMO047a_DS2	0.3491	0.3491	0.3491
304	5708	Sandpiper Pipeline GLHMO048a_DS	0.3669	0.3669	0.3669
304	5801	Sandpiper Pipeline GLHMO010a_DS3	0.3531	0.3531	0.3531
304	5802	Sandpiper Pipeline GLHMO010a_DS4	0.3495	0.3495	0.3495

ACU	Subpop #	Subpopulation Name	pP-Current	pP - Best	pP - Worst
296	5901	Near jct 36N & 144W, S of 36N	0.6507	0.6520	0.6309
296	5902	About 1.0 km NW jct 36N & 145W, near 145W	0.1496	0.1512	0.1240
296	5903	Grande Clairière	0.5659	0.5679	0.5328
296	6001	West of jct 36N & 145W, N and S of 36N	0.3218	0.3223	0.3164
296	6101	1.0 km W jct Hwy 2 & 145W, N of Hwy 2	0.5372	0.5386	0.5144
296	6301	2.0 km N jct 254 & 541, E of 254	0.6993	0.7064	0.6929
296	6401	0.5 km S jct 543 & 254, W of 254	0.7942	0.7957	0.7725
296	6402	Along 43N, E of 254, N of 43N	0.7140	0.7151	0.6955
296	6403	Along 43N, E of 254, S of 43N	0.1496	0.1512	0.1240
296	6404	Off 139W, N of jct 139W & 46N, E of 139W	0.1322	0.1330	0.1198
296	6405	Near jct 41N & 254, W of 254	0.6209	0.6221	0.5996
296	6501	Sifton 1	0.2294	0.2305	0.2294
296	6502	Sifton 2	0.7140	0.7153	0.6955
296	6503	Sifton 1 H - OK14	0.7140	0.7151	0.6955
296	6601	Andersons Meadow	0.2239	0.2234	0.2246
296	6602	Smokey Lake	0.5420	0.5431	0.5398
296	6603	Smokey Lake School Sec.	0.5171	0.5243	0.4985
296	6701	10.0 km N of Portal on south facing bank	0.4407	0.4742	0.4314
296	6801	15.0 km SSW of Frobisher, above Souris River	0.4465	0.4568	0.4314
296	6802	Area S of Coalfields Community Pasture	0.4465	0.4568	0.4314
296	6901	Camp Grafton	0.3547	0.3547	0.3547
296	7002	About 8 km E of Roche Percee, S of Souris River	0.4436	0.4565	0.4314
296	7003	About 5 km E of Roche Percee	0.4602	0.4671	0.4365
296	7004	8.0-9.6 km E. of Roche Percee above Souris River	0.3729	0.3766	0.3491

ACU	Subpop #	Subpopulation Name	pP- Current	pP - Best	pP - Worst
296	7005	Along road N of Souris River	0.7140	0.7170	0.6972
296	7006	N of road adjacent to Souris River, Site 1	0.4871	0.4940	0.4422
296	7007	Near Longney's Crossing, N of Souris River	0.4871	0.4940	0.4422
285	7101	St. Laurent 4	0.4792	0.4810	0.4509
285	7201	St. Laurent 1	0.3905	0.3929	0.3520
285	7202	St. Laurent 5	0.3905	0.3929	0.3520
285	7301	St. Laurent 2	0.5751	0.5759	0.5623
285	7302	St. Laurent 3	0.4792	0.4810	0.4509
296	7401	Towner East	0.1218	0.1207	0.1184
296	7402	Towner West	0.1184	0.1196	0.1165
304	7501	McKenzie District - Krych	0.3547	0.3547	0.3504
304	7601	DAPL 8	0.1828	0.1828	0.1828
304	7701	Garrison_Training_Area	0.2300	0.2300	0.2300