Craig Dremann, Box 361, Redwood City, California 94064 - (650) 325-7333

Jennifer O'Brion
U. S. Fish and Wildlife Service
Portland Regional Office
Division of Endangered Species
911 NE. 11th Avenue
Portland, Oregon 97232-4181

June 28, 2002

Dear Ms. ~~O'Brion~~ Baro,

I mailed four petitions on June 18, 2002, which were received by your office the morning of June 20, to list two grasses *Bromus arizonicus* and *Nassella cernua*, and one to list the Sage Grouse, and another to upgrade the listing for the Desert Tortoise from Threatened to Endangered.

I am re-submitting the four petitions, to add the date to each of them, and to correct two parts of the *Bromus arizonicus* petition: a typo in the first paragraph under rainfall where "(cm)" was accidentally added, and to add the citation under Literature Cited for the Flora of Kern County.

Do I understand correctly, that the ruling of the U.S. District Judge Vaughn Walker of San Francisco, on Friday, June 21, 2002, where he decided that Federal law requires the USFWS to decide within 90 days whether protection is needed for a petitioned species, and the Service must make a final decision on listing a year later, also applies to my four petitions and they will be processes within the legally required response time?

Sincerely,

Craig C. Dremann

Craig C. Dremann

RECEIVED
JUL - 2 2002
US FISH & WILDLIFE SERVICE
REGION 1, PORTLAND, OR

Petition to list Greater sage-grouse (Centrocercus urophasianus) as an Endangered Species.

This action is supported by substantial information that warrants this action, by the data listed in the publication "Greater Sage-Grouse and Sagebrush-Steppe Ecosystems Management Guidelines" (Barrett, Hugh, et al. 2000), which is quoted herein:

Sage-grouse populations have exhibited long-term declines throughout North America, declining by 33 percent over the past 30 to 40 years (Braun 1998). The species has been extirpated in five states and one Canadian province, and is "at risk" in six other states and two Canadian provinces. Even in the five Western states where the species is considered to be more abundant, long-term population declines have averaged 30 percent (Connelly and Braun 1997, Crawford and Lutz 1985). Various factors affecting sage-grouse populations occur at different temporal and spatial scales. No single causal factor has been identified for these declines. Instead, an accumulation of factors described herein are responsible.

Historically, around 220 million acres of sagebrush-steppe vegetation types existed in North America (McArthur and Ott 1996), making it one of the most widespread habitats in the country. Much of this habitat, however, has been lost or degraded over the last 100 years. For example, in the interior Columbia River Basin, total acreage in sagebrush-steppe habitat has been reduced from about 40 million acres to 26 million acres, representing a loss of about 35 percent since the early 1900s (Hann et al. 1997). Most remaining sagebrush-steppe ecosystems in Oregon are on public lands managed by BLM. Sage-grouse have been extirpated in five states (Arizona, New Mexico, Oklahoma, Kansas, and Nebraska) and British Columbia and is "at risk" in six states (Washington, California, Utah, Colorado, North Dakota, and South Dakota) and in the Canadian provinces of Alberta and Saskatchewan. In five states (Oregon, Nevada, Idaho, Wyoming, and Montana), long-term population declines have averaged 30 percent since 1950.

Threats to the Species As discussed below, numerous activities have adversely impacted, and continue to have potential to adversely impact, the distribution and quality of sage-grouse and their habitat. In addition, natural events and the human response to them could directly impact sage-grouse, as well as their habitat.

Agricultural conversion. Permanent conversion of sagebrush to agricultural lands is the single greatest cause of decline in sagebrush-steppe habitat in the interior Columbia Basin (Quigley and Arbelbide 1997). In the northern half of eastern Oregon, large areas of sagebrush-steppe habitat have been converted to agricultural lands (Wisdom et al. in press). Although sage-grouse do use some agricultural lands (such as alfalfa) for brood-rearing habitat, row crops are not beneficial habitat (Blus et al. 1989).

Rangeland conversion. Prior to the 1980s, herbicide treatment of large tracts of rangeland (primarily 2,4-D) was a common method of reducing sagebrush (Braun 1987). In many cases, broad herbicide treatment may have contributed to declines in sage-grouse breeding populations (Enyeart 1956, Higby 1969, Peterson 1970, Wallestad 1975). A Utah study suggests that this adverse impact on sage-grouse was compounded in areas subsequently reseeded to crested wheatgrass (Agropyron cristatum) (Enyeart 1956). Mechanical treatments (mowing, plowing, and chaining) of sagebrush have generally been more "local" in nature, but these, too, have adversely impacted sage-grouse habitat if done on a broad scale (Swensen et al. 1987). Even small-scale projects to reduce sagebrush can be damaging if in the wrong location, such as in winter habitat.

Livestock management. Various livestock management practices have altered sage-grouse habitat over the last century. Livestock facilities such as spring developments, water pipelines, and fencing have distributed livestock use over areas formerly used only sporadically or lightly. In many areas, grazing has contributed to long-term changes in plant communities and reduced certain habitat components, such as biological crusts that contribute to the health of sagebrush-steppe habitat (Mack and Thompson 1982, Quigley and Arbelbide 1997, Wisdom et al. in press). Grazing too soon after disturbances such as fire may lead to long-term reductions in food plants and nesting cover. Current BLM policy provides for a minimum rest of two growing seasons following fire. Temporary, non-renewable use can result in removal of residual grass and the herbaceous plants needed for nesting cover. Past land treatments have included seedings, many of which did not include sagebrush, native forbs, and native grasses. This kind of seeding activity contributes to an increased dominance of exotic species that are detrimental to sage-grouse habitat. Drought can lead to an increase in overlapping use among livestock, wild horses, and sage-grouse. Drought can exacerbate adverse effects of livestock and wild horse grazing on vegetation and soils (Valentine 1990). In some instances, failure to timely adjust livestock use during drought has resulted in limited plant regrowth and overuse in wet meadows and riparian areas, negating gains in rangeland conditions during higher-precipitation years (Thurow and Taylor 1999). Grazing management is guided by land use plans and specific allotment management plans. In addition, grazing management practices will be applied to attain the Standards for Rangeland Health. Standard 5 specifically addresses protecting threatened and endangered and special status species. If it is determined that the rangeland health standards, including Standard 5, are not being met, appropriate changes in grazing management will be implemented prior to the next grazing year to ensure significant progress towards attainment of habitat objectives and the standards of rangeland health.

Wildfire and prescribed fire. Fire has altered sage-grouse habitat on the landscape in Oregon. Sagebrush plants, especially Wyoming big sagebrush plants,

are vulnerable to fire. Existing BLM fire management plans have not, for the most part, identified sage-grouse habitat as a high priority for protection. Furthermore, during multiple fire events, which are common in sagebrush-steppe habitat, prompt access to local BLM resource specialists knowledge-able about the location of critical sage-grouse habitat areas may be limited. Historical fire suppression tactics of "burning out" the unburned interior islands within fire perimeters has resulted in additional loss of habitat and loss of seed sources within the core area. Repeated wildfires have favored invasion by cheatgrass (Bromus tectorum) and other exotic species (Pellant 1990, Valentine 1990). Conversion to cheatgrass alters the fire frequency from the historic 32- 70 years in sagebrush-steppe ecosystems to 5 years or less (Wright and others 1979). In this scenario, referred to by Pellant (1996) as the cheatgrass-wildfire cycle, the risk from wildfire is very high and fire suppression efforts are challenged by very high spread rates. This situation has increased the potential for large fires, carrying a threat for additional cheatgrass invasion onto adjacent areas not yet dominated by cheatgrass. Prescribed fire has also contributed to the decrease in Wyoming big sagebrush habitat and sage-grouse brood-rearing habitat (Connelly et al. 1994, Fischer et al. 1996a). The Federal Wildland Fire Management Policy and Program Review (USDI and USDA 1995) indicates that, consistent with land and resource management plans, fire must be reintroduced into the ecosystem to restore and maintain ecosystem health and reduce wildfire risk. Recent budget increases in fuels management has resulted in the increased use of prescribed fire and other fuels management treatments.

Fire rehabilitation. The lack of prompt and appropriate fire rehabilitation following a wildfire can present additional threats to sage-grouse habitat. The seed supply of native species is generally limited during years of extreme fire when large acreages burn. Although the planting of brush species is more common now than in the past, sagebrush may not always be included in all rangeland fire rehabilitation seeding mixtures. Crested wheatgrass is often planted in lieu of native species or as a mixture with native species, because it is readily available and can successfully compete with cheat-grass. If cheatgrass or any of a number of other exotic plant species are present before a fire occurs, they are likely to become more dominant afterwards if the area is not properly rehabilitated.

Structures. Power lines, fences, roads, and urban development have all had an adverse impact on sage-grouse habitat and their populations (Braun 1998). Roads and associated human disturbances can have adverse impacts, especially to lek and winter habitat areas (Wisdom et al. in press). Power lines and fences provide perches for birds of prey and may actually cause direct mortality when sage-grouse fly into them (Connelly pers. comm.). Urban development results in direct loss due to fragmentation of habitat.

Juniper expansion. Before settlement by Euro-Americans, western juniper (Juniperus occidentalis) existed in open, savannah-like woodlands maintained by relatively frequent fires (Nichol 1937 in Miller and Rose 1995, West 1988 in Miller and Rose 1995) or were confined to rocky surfaces or ridges (Barney and Frishknecht 1974, Cottam and Stewart 1940, and Johnson and Simon 1987 in Miller and Rose 1995). These woodlands had an understory that included various sagebrush species. Since the 1880s, western juniper has expanded into mountain big sagebrush, low sage brush (A. arbuscula), quaking aspen (Populus tremuloides), and riparian communities (Miller and Rose 1995). The extent of the juniper-sagebrush cover type within the Columbia Basin more than doubled over the past century (Quigley and Arbelbide 1997). Increased livestock grazing in the late 1800s and early 1900s contributed to a reduction in fuels that could carry fire, thereby decreasing fire frequency (Eddleman and others 1994). In addition, fire suppression policies have generally lengthened fire-return intervals in juniper-dominated areas. Although restoring lands dominated by western juniper could benefit sage-grouse, certain types of post-treatment management could result in cheatgrass invasion, which would adversely impact native plant recovery. Also, while juniper may make poor habitat for sage-grouse and the reduction of juniper would be beneficial for them, we must be careful to adequately provide for the habitat needs of juniper-associated sensitive species such as the gray flycatcher (Empidonax wrightii).

Exotic invasive plants. Although cheatgrass proliferation has been widespread, increases in other exotic species such as medusahead (Taeniatherum caput-medusae), knapweed (Centaurea spp.) and yellow starthistle (Centaurea solstitialis) are also adversely impacting sagebrush-steppe habitat (Quigley and Arbelbide 1997). Many exotic plants are adapted to the Great Basin climate (Trewartha 1981 in Mack 1986, Young and others 1972 in Mack 1986). The rapid rate of expansion is partly attributable to the life history of exotic plants. Exotic plants are often opportunists, and many are pioneer, colonizing species. They are frequently one of the first species to arrive and colonize areas that have experienced soil-surface disturbance or areas that lack plant cover. Their establishment and spread are aided by disturbance to the soil surface (Baker 1986, Bazzaz 1986). Spotted knapweed (C. maculosa), yellow starthistle, and leafy spurge (Euphorbia esula), however, have exhibited the ability to invade relatively undisturbed sites, including wilderness areas (Asher 1994, Tyser and Key 1988).

Wild horses. Excessive grazing by wild horses has contributed to a decline in sage-grouse habitat over the last century. In some areas, grazing by wild horses has contributed to long-term changes in plant communities and reduced certain habitat components such as biological crusts, which contribute to the health of sagebrush-steppe habitat (Mack and Thompson 1982, Quigley and Arbelbide 1997, Wisdom et al. in press). Wild horses are managed by the BLM in 20 Herd Management Areas encompassing 2.8 million acres of public lands located primarily in southeastern Oregon. The cumulative Appropriate Management

Level for horse numbers in these areas is 1,351 to 2,650 animals. The management goals for wild horses are to manage them as components of the public lands and in a manner that preserves and maintains a thriving natural ecological balance in a multiple use relationship.

Illegal sowing of exotics after fire. The petitioner add the illegal sowing of exotics by Federal land managers after fire, without the writing of the required NEPA documents , which outlines the impact that the exotics will have on the wildlife and ecosystem.

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Respectfully submitted,

Craig C. Dremann

Craig C. Dremann, P.O. Box 361, Redwood City, CA 94064 (650) 325-7333

RECEIVED
JUN 20 2002
US FISH & WILDLIFE SERVICE
REGION 1, PORTLAND, OR

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Pledge
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cc:
Hot Bob
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Institute for Wildlife Protection
Office of Species Protection – Eugene, Oregon
Office of Ecosystem Protection – Richmond, Vermont
Office of International Affairs – Olympia, Washington
Office of Forest Conservation – Eugene, Oregon

541/434-6630 VOICE
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Office of Species Protection
2630 Elinor St.
Eugene, OR 97404

March 19, 2003

Anne Badgley, Regional Director
U.S. Fish and Wildlife Service
911 NE 11th Ave.
Portland, OR 97232-4181

Dear Regional Director Badgley.

The Institute understands that the US Fish and Wildlife Service is adopting the position that there are no legal subspecies of the Northern (Greater Sage Grouse). We believe that this position is incorrect and are involved in challenging that position in court. However, in order to protect sage grouse in the event that a court determines that the Service can disallow these designated subspecies, we are now petitioning the entire species for listing under the Endangered Species Act. We continue to believe that the listing of sage grouse by subspecies affords the Service management flexibility, but we will ensure that sage grouse are protected. The Northern or Greater Sage Grouse (*Centrocercus urophasianus*) has been the subject of two previous petitions from the Institute – one for the Western subspecies, and one for the Eastern subspecies. We incorporate those previous petitions into the present petition for the entire species. For the reasons stated in the previously submitted petitions (incorporated by reference herein) as well as the supplemental information provided below, the Institute is requesting a listing as endangered. The previous petitions submitted to you are:

Webb, R. 2001. Status Review of the Western subspecies of the Greater Sage Grouse (*Centrocercus urophasianus phaios*). Publ. No. 024-02 of the Institute for Wildlife Protection; Office of Species Protection; 2630 Elinor St.; Eugene, OR.

Webb, R. 2002. Status Review of the Eastern subspecies of the Greater Sage Grouse (*Centrocercus urophasianus urophasianus*). Publ. No. 186-02 of the Institute for Wildlife Protection; Office of Species Protection; 2630 Elinor St.; Eugene, OR.

To summarize our previous submissions: Sage grouse have declined from an estimated 2 million or more birds to only about 100,000 or fewer today. Numbers have not stabilized, and these declines are continuing. Significant declines have taken place in the last decade. Habitat has been degraded, highly fragmented, and drastically reduced. Climate change will cause almost complete elimination of all sagebrush in the United States within the foreseeable future. Agriculture, fire, spraying of pesticides, cattle grazing, development, fencing, juniper and pinion pine intrusion, power lines, roads and energy developments threaten sage grouse. The two previous petitions noted above provide abundant evidence and citation to the scientific literature regarding these threats.

We additionally supplement the information in the previous petitions with the following:

Based on a Masters thesis by one of John Crawford's students at Oregon State Univ., there are indications that SG hens will not return to burned sites for 40 years or more. This increases the threat to sage grouse viability from range fires.

Land management agencies are not following the guidelines established by scientists with expertise on sage grouse; instead, "agencies pick and choose which guidelines to follow and vary their application among states, districts, and resource areas or virtually ignore" the guidelines (Braun, Oedekoven, Aldridge 2002, p. 13).

The "impacts of oil and gas development have been and are negative for sage-grouse," and sage grouse will be "at risk of local extirpation in intensively developed areas" (Braun, Oedekoven, Aldridge 2002, p. 12, 13).

Viability is not linear with environmental conditions. Instead, populations can appear relatively stable over a wide range of conditions, and then "decline rapidly toward extinction" with only small additional declines" (Adams 2002).

Development is a severe threat to sage grouse habitat. A study by the American Farmland Trust (2002) shows that 25 million acres of rangeland will be threatened by sprawl and low density development in the next 20 years; moreover, the greatest risk is to the most productive sage grouse habitats.

Habitat fragmentation from agriculture strongly increased nest predation -- nests in fragmented landscapes are about 9 times more likely to be depredated as those in continuous landscapes (Vander Haegen, et al. 2002)

The Service must carefully consider inbreeding effects, because ignoring "inbreeding depression will substantially underestimate extinction risk," and mean time to extinction can easily diminish by 30% (Brook, et al. 2002).

Extinction of sage grouse from the ICBEMP analysis area (Interior Columbia Basin) is highly likely within 100 years under present management directions (Wisdom, Rowland, et al. 2002). There is a moderate probability of extinction in the area even if environmental conditions do not deteriorate from those of the present (Wisdom, Rowland, et al. 2002). Local restoration efforts are unlikely to prevent extinction in the area (Wisdom, Rowland, et al. 2002, p. 1230). The risk of extinction will be reduced only if restoration of habitat is successful in a coordinated and comprehensive manner at regional scales (Wisdom, Rowland, et al. 2002, p. 1230).

Habitat restoration, however, is unlikely to occur. A single factor, the effects of exotic plants – notably cheatgrass (*Bromus tectorum*) – makes restoration unlikely directions (Wisdom, Rowland, et al. 2002, p. 1230). The amount of sage grouse habitat in the ICBEMP analysis area (Interior Columbia Basin) will decline by 17% to 19% within the next 100 years even with significant reductions in livestock grazing and active ecosystem restoration (Hemstrom, et al. 2002). Restoration will require "monumental" efforts both in terms of the vast spatial extent of restoration and in terms of the lengthy time periods over which restoration will have to be conducted (Hemstrom, et al. 2002, p. 1253). Thus, restoration is unlikely to succeed and habitat will declines will be even worse. Sage grouse habitat is "susceptible to a dramatic acceleration in loss and degradation" (Hemstrom, et al. 2002, p. 1253), leading to rapid extinction of sage grouse from the area.

Johnsgard (2002) argues that hunting is a major threat to sage grouse. The Institute has discussed this thoroughly in the petitions referenced above. The Service

must carefully examine this issue in making a listing decision, designating critical habitat, and in its other duties under the ESA. As a first estimate, the Institute believes that hunting should be prohibited for Gunnison and Mono sage grouse as well as the DPS in Washington state. Further, hunting should be prohibited on the margins of the range for all sage grouse; however, limited hunting may be appropriate – even after listing – for a few populations in relatively remote areas with good reproductive output.

We enclose a list of additional Bibliographic references for your convenience.

You are required to acknowledge receipt of this petition in writing within 30 days. 50 C.F.R. § 424.14(a).

Sincerely,

Don Webb

Don Webb, Staff Attorney

Enclosure: Additional Literature on Sage Grouse and Threats to their Existence

Additional Literature on Sage Grouse and Threats to their Existence

Adams, P. A. 2002. Will small population sizes warn us of impending extinctions? Amer. Natur. 160(3): 293-305.

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Bob Behan x AES

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Institute for Wildlife Protection

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Office of Species Protection – Eugene, Oregon
Office of Ecosystem Protection – Laurel Hill, Oregon
Office of International Affairs – Olympia, Washington

Office of Species Protection
2630 Elinor St.
Eugene, OR 97404

July 3, 2002

Anne Badgley, Regional Director, U.S. Fish and Wildlife Service
911 NE 11th Ave.
Portland, OR 97232-4181

Dear Regional Director Badgley:

Enclosed please find a Status Review and Petition for a Rule to List the Eastern sage grouse under the Endangered Species Act. Petitioners submit this petition pursuant to the Endangered Species Act and Administrative Procedures Act. We are requesting a listing as Endangered. Endangered means in danger of extinction in all or a part of its range. Neither Congress nor the Service has defined danger; however, it is clear that the Eastern sage grouse are endangered using the definitions of danger in Webster's International Dictionary or in Black's Law Dictionary.

You are required to designate critical habitat at the time of listing. Many ranchers have expressed fear regarding the economic consequences to them of a sage grouse listing. You are not allowed to consider economic effects when listing a species but may do so when designating critical habitat. The Institute requests that you consider the economic effects of critical habitat designations on small ranchers. An analysis of federal grazing permits by reporters Paul Rogers and Jennifer LaFleur of the San Jose Mercury shows that the top 10% of grazing-permit holders control a striking 65% of all livestock on BLM property and 49% of the livestock on USFS lands (San Jose Mercury, Nov. 7, 1999; Deseret News, Sunday, November 28, 1999). Therefore, consideration of effects of designating critical habitat on small ranchers will have little effect on sage grouse. The Institute will monitor critical habitat designations to ensure that they are adequately protective of sage grouse. As The Deseret News put it "wealthy hobby ranchers, agribusiness giants and corporations" are the major beneficiaries of public lands grazing. Thus, consideration of effects of designating critical habitat on small ranchers would most likely benefit the overall US economy by reducing subsidies to those that do not need them.

We believe you will find this status review and petition to be extensive, thorough, and comprehensive. Our Olympia, Washington office is designated as the lead for this status review and petition; however, for simplicity please route all your contacts through our Eugene, Oregon office. In order to reduce the workload on the Service, Institute staff have attempted to encompass all information relevant to a listing in the enclosed status review. We welcome your prompt attention to this matter. The Institute maintains an extensive library and documents collection. If you require any documents cited by us in order to complete your review, and are unable to otherwise obtain them, please contact us, as we may be able to supply them. We assume that the Service has ready access to published sources as well as government documents. These documents were prepared under the direction of Dr. Steven G. Herman at our Olympia office. However, please contact me (at the address or telephone number above) if you need any assistance. We want to do everything possible to help you complete your review as quickly as possible, and within the statutory time limits. Best wishes for an enjoyable Fourth of July Celebration.

Sincerely,

Don Webb

Don Webb

Status Review: Eastern Sage Grouse

Status Review of the Eastern subspecies of the Greater Sage Grouse (*Centrocercus urophasianus urophasianus*)

Prepared by:

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Abstract

The Eastern sage grouse is a recognized subspecies of the Greater (or Northern) sage grouse with the scientific name *Centrocercus urophasianus phaios*. The range of the Eastern sage grouse and the number of individuals has decreased alarmingly, and the subspecies has become isolated into a series of fragments. Sage grouse once numbered in the millions or tens of millions – today, barely 100,000 birds remain. Although this appears at first glance to be a relatively large number of individuals, sage grouse are spread thinly over vast areas of degraded habitat, and are subdivided into numerous separate populations. Like water in a large, shallow skillet, the birds will soon evaporate from the landscape. Two threats are individually capable of causing extinction: the spread of juniper trees and cheatgrass invasion. Both these threats are generated by climate change and by livestock grazing. Junipers serve as raptor perches, creating kill zones for sage grouse. Juniper is projected to cover almost all current sage grouse habitat within this century, causing extinction. Cheatgrass is spreading rapidly through the sagebrush habitat required by sage grouse, and kills sagebrush by increasing fire frequency.

Introduction

In historical times, sage grouse were so numerous that their flocks used to darken the skies (Patterson 1952c, p. 19). Vast clouds of the birds extended for miles. Today, the bird has been extirpated from 5 states, and is "at risk" in 6 other states (Bradley 1999; Nevada State

Office, BLM 2000a, p. 1) and only remnant populations exist even in the center of the range. Existing populations are highly fragmented, and population trends are downward even among the largest populations. All remaining habitat has been degraded. Sage grouse inhabit the sagebrush shrub-steppe areas of North America, a little-loved landscape that has been severely damaged by a wide variety of threats. Vast areas of the public's land has been converted to pasturage with exotic plant species, water pipes and troughs, and electric pumps – the infrastructure of industrial agriculture needed to support livestock management. Agriculture occupies 41% of the areas from which sage grouse have been extirpated in the interior Columbia River basin (Wisdom, Wales, et al. undated, p. 12) – this simple statistic illustrates the extreme effect of agro-industrial infrastructure on sage grouse.

Here, I review the status of sage grouse, its vulnerability to extinction, the demise of its habitat, and the malfeasant actions of state and federal agencies who were supposed to protect the puclic's lands and the public's wildlife. This Status Review incorporates by reference all citations in the Bibliography (Webb and Salvo 2001), as well as the citations in the references themselves. The Service recognizes that it must examine "information submit[ted] with or referenced in the petition" (Deibert 1999b). The Bibliography consists of the literature cited and selected references, which are intended to help the Service in its evaluation of the plight of this species.

Taxonomy

The two species of sage grouse, the Gunnison sage grouse, with the proposed binomial *Centrocercus minimus*, and the Greater (or Northern) sage grouse, *Centrocercus urophasianus* (Bonaparte 1827), are referred to the family Phasianidae (formerly to the family Tetraonidae), in the order Galliformes (AOU 1998, p. 118-119; Sibley and Monroe 1990, 1993, p. 23). The first written accounts of the species are from the Lewis and Clark expedition in 1805 (Thwaites 1959). The species was formally described in 1827 (*Tetrao urophasianus*) by C. L. Bonaparte, and was revised and placed in the monotypic genus *Centrocercus* by Swainson and Richardson (1831). In the 1990s it became obvious that *C. minimus* deserved species rank (Braun and Young 1995; J. R. Young, et al. 2000; summary in Webb 2000). The Greater sage grouse is divided into two subspecies, the Western and the Eastern. The AOU recently officially recognized the species status of the Gunnison sage grouse and renamed the Northern sage grouse to "Greater sage-grouse" (AOU 2000). Scientists working directly with sage grouse intend to appeal the renaming of Northern to Greater sage-grouse. This report will thus continue using the common name Northern sage grouse for *Centrocercus urophasianus*.

Common Names

The standardized common names are Gunnison sage grouse and Greater or Northern sage grouse but the species have also been referred to variously as sage hen, sage cock, spiny-tailed pheasant, spine-tail grouse, fool hen, cock of the plains, tétras des armoises (French), Beifusshuhn (German) or sage chicken (Coues 1893; Girard 1937; Patterson 1952c; Jewett, et al. 1953; Johnsgard 1973, p. 155; Johnsgard 1983, p. 109). Lewis and Clark used the term "Cock of the Plains" (Terres 1980). Male sage grouse have been called toms, mountain cocks, master-of-the-plains, old toms, bustards, prairie turkeys, heath cocks, sage fowls, turkey gobblers, sergeant-at-arms, and turkey buzzards, while females have been called brush hens, battle hens, and heath

hens (Girard 1937). Together with sharp-tailed grouse (*Tympanuchus phasianellus*), sage grouse are sometimes popularly termed prairie grouse. Various Native Tribes and language groups used a number of different names to refer to sage grouse, including such phonemic Anglicizations as Kop-te, Ko-pah-te, Hoo-dze-hah, Oo-jah, Se-chah, Witch-ah, See-yook, and more (Merriam 1979). The standard AOU (American Ornithologists' Union) code for the Northern (Greater) sage grouse is CEUR [309].

Affinities of Higher Taxa

Sage grouse are taxonomically distinctive and *Centrocercus* is a designated subgenus (AOU 1998). Bonaparte (1827) first described a single species as *Tetrao urophasianus*, and the genus was revised to *Centrocercus* in 1831 (Patterson 1952c). Short (1967) recognized a Subfamily, Tetraoninae, containing sage grouse and allied species. Sibley and Monroe (1990, p. 11) followed Short's general sequence of species in the Phasianidae. The AOU recognizes the Tetraoninae, following Ellsworth, et al. (1995, 1996).

Hudson, et al. (1964) proposed that sage grouse were most closely related to species of forest grouse, rather than to sharp-tailed grouse or other prairie dwelling birds. Johnsgard (1973) followed Holman (1964) in suggesting that speciation in these taxa followed increasing aridity, and that *Centrocercus* is most closely related to a genus of forest dwelling grouse, *Dendragapus*. This assertion was supported by the mt-DNA work of Ellsworth, et al. (1995). This scheme differs somewhat from that of Short (1967) who proposed that sage grouse are most closely related to *Dendragapus obscurus*, the Blue Grouse. Lumsden (1968) supported this view based on behavioral similarities, and Johnsgard (1973) supported it based on adult and downy plumage characteristics. The taxonomic affinities assigned by these studies roughly parallel those of Sibley and Monroe (1990, 1993). Interestingly, the mating systems of sage grouse and other grouse appear to have evolved independently (Ellsworth, et al. 1995, p. 498).

The oldest fossils of the Galliformes date from the middle Eocene (Kuz'mina 1992). The Phasianids are the largest family in the order and are predominately found in tropical and sub-tropical areas (Kuz'mina 1992). Tetraoninae are endemic to the Holarctic with 18-21 widely distributed species (Kuz'mina 1992). Mayr (1946) and Short (1967) ascribed the origin of the Tetraoninae to North America. However, the greatest diversity of Phasianids is in southern Asia, and a total of about 160 species are assigned to the family. There are 10 species of grouse in North America (Braun, et al. 1994).

DNA hybridization techniques and electrophoretic analyses of egg albumins show a close relation of grouse and pheasants, with a possible divergence during the Miocene (del Hoyo, et al. 1992).

Sage grouse hybridize rarely with sharp-tailed grouse (*Tympanuchus phasianellus*) and blue grouse (*Dendragapus obscurus*) (Johnsgard 1983; Aldridge, et al. 2001). The Northern sage grouse is the largest grouse in North America, and except for the Eurasian Capercaillie species, the largest grouse on Earth (Johnsgard 1983).

Use of Information on Sage Grouse species and subspecies

All available data indicate that the ecological traits and habitat needs of Gunnison sage grouse are virtually identical to those of Northern sage grouse (J. R. Young 1994b, p. 44). This review will thus use data on the Gunnison species for those issues. J. R. Young (1994b, p. 44)

identified only two habitat type and ecological traits differing between the species: Gunnison sage grouse are more tolerant of trees during the nesting and brooding stages, and Gunnison females have a lower rate of renesting than do female Northern sage grouse (thereby increasing the threat of population extinction from individual nest failure). The tolerance of trees by Gunnison sage grouse may reduce the impact of juniper invasion on this species; however, it might also merely be a response to severe habitat loss, thus exposing the Gunnison females to even higher mortality and nest failure. The latter seems likely as the birds in Young's study were affected by "heavy grazing and drought" and production of young was low (J. R. Young 1994b, p. 45). Likewise, this review will use basic biological information on both subspecies of the Northern sage grouse, and will use the term "sage grouse" to refer to either subspecies or either species interchangeably, unless otherwise noted.

Subspecies of the Greater (or Northern) Sage Grouse

There are two recognized subspecies of the Northern sage grouse as described by Aldrich (1946) and Aldrich and Duvall (1955): the Eastern sage grouse, *Centrocercus urophasianus urophasianus*, and the Western sage grouse, *Centrocercus urophasianus phaios* Aldrich (AOU 1983; Schroeder, et al. 1999a). The subspecies were first recognized by the AOU (American Ornithologists Union) in 1957. The AOU is the recognized scientific organization for the recognition of avian taxonomy and nomenclature in the United States. The Service is aware that the AOU "recognizes a western and eastern subspecies of the (non-Gunnison) northern sage grouse" (Long 1999a; see also FWS 2001d, 66 Fed. Reg. 22984, 22985). The AOU is unlikely to change this designation as the Committee on Taxonomy requires the publication of "substantial and convincing evidence" before a change is made (AOU 2000, p. 847). Aldrich (1946, p. 129) established the Western subspecies based on 11 specimens taken from 8 locations (5 from Oregon, 2 from Washington, and 1 from California), referring the rest of the range to the Eastern subspecies. Although the sample size is low, Aldrich traveled widely and visually observed a larger number of birds from 35 locations (Aldrich 1992). Aldrich also stated that he is quite sure of the subspecies designation (Aldrich 1992). In 1955, Aldrich and Duvall listed a number of other specimens that were reported in the literature and in correspondence to them (Aldrich and Duvall 1955, p. 2).

The designation of these two subspecies has been criticized (Johnsgard 1983) but has not been rescinded (AOU 1998; Schroeder, et al. 1999a; Drut 1994, p. 2). Neither the duly recognized scientific body charged with systematics and taxonomic designation in birds (the AOU Committee on Classification and Nomenclature) nor the Service itself has questioned the subspecies designation for sage grouse. Banks (2001), who is a FWS employee and chairman of the Classification Committee, noted that "there were no serious taxonomic problems" with the subspecies designation. Banks also believes that management purposes will be furthered if the subspecies continues to be recognized (Banks 2000). Nonetheless, it may be that additional scientific studies will support elimination of this designated subspecies at some time in the future.

According to preliminary reports, one genetic study has failed to support a subspecies split within the Northern sage grouse. This study has not been published, and has not undergone peer review (and thus must receive reduced weight from the Service under its Substantial Information Policy). Moreover, both the project leader for this study (Dr. Tom Quinn), as well

as most other geneticists, recognize that genetic data alone should generally not serve to designate or de-designate taxonomic ranks (Quinn 2000).

The Service itself has also recognized the separate subspecies of the Northern sage grouse. The earliest official recognition was in a 1955 publication in which the Service surveyed the status of a wide variety of gallinaceous game birds (Aldrich and Duvall 1955). Published under the aegis of then Director Farley, this Service publication delineated the range of the Western subspecies as had Aldrich (1946), but included a slightly larger part of central western Idaho as being within the range of the Western sage grouse (Aldrich and Duvall 1955, map, p. 12).

The Service designated the Western subspecies of the Northern Sage Grouse as a Category 2 (C2) species for consideration for listing under the ESA on Sept. 18, 1985 (50 Fed. Reg. 58454). The C2 category consisted of species for which listing may be warranted, but "conclusive" data not yet gathered) after noting that it was declining. The Service listed the Western sage grouse as a C2 species in the subsequent Candidate Notices of Review: Jan. 6, 1989 (54 Fed. Reg. 554), Nov. 21, 1991 (56 Fed. Reg. 58804), and Nov. 15, 1994 (59 Fed. Reg. 58982). On Feb. 28, 1996, the Service completely eliminated the entire candidate ranking system (61 Fed. Reg. 7596), removing any legal protection for the Western sage grouse as well as the more than 3,600 other species on the C2 list. Even after elimination of the C2 list, the Service has consistently recognized the Western subspecies. For example, on August 10, 1992, the Western Field Supervisor for the Service, David C. Frederick, signed the "Conservation Agreement – Western Sage Grouse" for the Yakima Training Center in the state of Washington (YTC CA 1992). A similar "Conservation Agreement – Western Sage Grouse" was signed by Mr. Frederick on March 5, 1994 (YTC CA 1994). More recently, the Service issued a finding on the Columbia Basin distinct population segment (DPS) of the Western subspecies of sage grouse (FWS 2001d; 66 Fed. Reg. 22984). The Service has noted that there are "behavioral differences" between the Western sage grouse and the Eastern sage grouse subspecies, "which are extremely important for reproductive efforts" (US Fish and Wildlife Service 1998, p. 1 of attachment entitled "Sage Grouse – (Candidate Conservation?)"). Service personnel have stated that they are "going to keep recognizing" the Western sage grouse as a subspecies, although the Service believes the case is weak (US Fish and Wildlife Service 1999, Rich Howard speaking, Jan. 25. Conference Call)

The Western subspecies occurs in Washington, central Oregon, California and a small portion of NE Nevada (Drut 1994, Fig. 1). Except for the intermediate forms in northern California and Nevada identified by the Service (Aldrich 1946, 1963), most of the range occurs within the Interior Columbia Basin and Great Basin. The largest remaining numbers of Western sage grouse occur in Oregon, and the subspecies cannot be recovered unless the Oregon birds are conserved. Only a few birds remain in Washington, and the intermediate forms in California and Nevada are too mixed, too endangered, and too few to provide adequate conservation of the Western sage grouse. Aldrich (1946) noted that the range possibly extended into a small portion of west central Idaho, and later (Aldrich 1963) appeared to locate the range of the Western subspecies into a small portion of Idaho. Only a miniscule number of these birds remain and they are isolated.

The Eastern subspecies occurs in eastern Oregon, California, Nevada, Colorado, Idaho, Utah, Wyoming, Montana, South Dakota and North Dakota. It formerly occurred in Oklahoma,

New Mexico, Arizona, Texas, Kansas, Nebraska, and 3 Canadian provinces until it was extirpated from those regions (Drut 1994, Fig. 1). Sage grouse have also been extirpated from most of North and South Dakota, all except the extreme northwestern tip of Arizona, and central California (Hamerstrom and Hamerstrom 1961; Ihli, et al. 1973). Eastern sage grouse occur in all states and provinces within the range of sage grouse except Washington (AOU 1983, Call and Maser 1985).

Description

Sage grouse are large, robust birds, characterized by considerable sexual dimorphism. In the Northern sage grouse, the body mass of females ranges from 1 to 2 kg, with lengths from 48 to 58 cm, while the body mass of males ranges from 2 to 3 kg, with lengths from 66 to 76 cm (Crunden 1963, Beck and Braun 1978).

Western sage grouse are generally darker than the Eastern subspecies (Aldrich 1946, p. 129; Jewett, et al. 1953). The Western sage grouse differs morphologically from the Eastern subspecies in having reduced white markings, darker grayish-brown feathering, and a more dusky overall appearance (FWS 2001d, 66 Fed. Reg. 22984, 22985). The subspecies differ in various other morphological and behavioral characters (Aldrich 1946).

In the smaller Gunnison sage grouse, the body mass of females ranges from 2 to 3 pounds [1.36 kg to 1.8 kg] and the body mass of males ranges from 3.3 to 4 pounds [1.5 kg to 1.82 kg] (Gunnison Basin Sage Grouse Conservation Plan (GBCP 1997, p. 3). Gunnison sage grouse are also morphologically distinguished from the Northern species by their longer, more distinct white barring of the tail feathers, and by bill shape and size (GBCP 1997, p. 3). Gunnison sage grouse are also characterized by a single genetic haplotype (GBCP 1997 p. 5). Both sexes have narrow, pointed tails, feathering to the base of the toes, and grayish brown, buff, and black variegated pattern on the upper body parts, with paler flanks, and diffuse black abdominal pattern (Johnsgard 1983). Schroeder, et al. (1999a) summarize the information on sage grouse species.

Sexual Dimorphism

During the breeding season, considerable color dimorphism exists between the sexes in both species (Johnsgard 1983, Braun 1991a, Patterson 1952c). Males have blackish brown throats that are separated from a dark "V" shaped pattern on the neck by a narrow white band. Males have expansive white breast feathers that conceal two large, frontally directed gular sacks of olive green skin, which the male inflates and deflates during sexual display (Dunn, et al. 1987). Short white feathers with stiffened shafts are located on the margins of the gular sacks and grade into softer and longer white feathers, and finally into a number of long black filoplumes. These hair like structures are erected during sexual display. Females lack these display features, have buffy throats with black markings, and have blackish brown barring on their lower throats and breasts. Additional accounts of sexual dimorphism are given by Honess and Allred (1942), Clark, et al. (1942), Crunden (1963), and Beck and Braun (1978). General descriptions can be found in standard guides such as Udvardy (1977), National Geographic Society (1987) and Harrison (1978), and in Dunn, et al. (1987), Girard (1937), Jewett, et al. (1953), Johnsgard (1973), among others.

Description of Life History Stages

Eggs are elliptical, semi-glossy, and pale olive to olive-buff with numerous small, dark-brown spots (Harrison 1978). Eggs weigh 38 to 41 grams, are 53 to 60 mm in length, and 36 to 41 mm wide (Patterson 1952c, O. C. Nelson 1955, Rothenmaier 1979).

Chicks are precocial with a mottled combination of black, brown, buff, and white feathers (Johnsgard 1973). The head is whitish and spotted with black and brown, while the underparts vary from grayish white to buff and brown, with a buff and brown band on the chest (Johnsgard 1973, Harrison 1978). Chicks have a black bill (Harrison 1978), black spots on the cheek and nostrils (Short 1967), and black spots on the lores (Harrison 1978). The downy plumage has a "salt and pepper" dorsal pattern (Johnsgard 1983).

Juveniles are distinguished by overall size and morphology, and more specifically, by the presence or absence of juvenile primaries 1 and 2, the condition of primaries 1, 2, 9, and 10, and the difference in length between primaries 2 and 3, depending on the stage of molt (Tirhi 1995). Juveniles also bear a sac-like structure on the dorsal surface of the cloaca, the bursa fabricii (Patterson 1952c). Sage grouse acquire full juvenile plumage between 6 and 8 weeks of age, at which time they resemble adult hens (Patterson 1952c). Juveniles are streaked on their upper body, and have brown and white wing coverts with white tips (Petrides 1942). The middles of the tail feathers are white as are the fringes (Ridgeway and Friedmann 1946).

Juveniles molt their wing and tail feathers 2 to 3 weeks after attaining juvenile plumage, and molt continues throughout the summer. The two outer primaries are maintained until after the mating season of the second year, but all other feathers are molted the first year. Juveniles can be identified by their frayed outer primaries. Sage grouse attain adult plumage after the first molt and molt to partial mating plumage in their first fall, reaching complete mating plumage the following spring.

Distinctiveness

Sage grouse are the only species of Phasianid living in desert shrub (Johnsgard 1983, p. 6). Sage grouse are uniquely adapted to the sagebrush shrub-steppe. The relationship to sagebrush is obligate and sage grouse require sagebrush for food. Sage grouse possess unique physiological and biochemical adaptations for the digestion and detoxification of sagebrush (Wambolt, et al. 1987; Welch, et al. 1989). These detoxification mechanisms make sage grouse of considerable importance for biomedical and genetic engineering research, particularly since monoterpenoids have bacteriostatic and bactericidal properties, and have been studied for use as prophylactic agents (Welch, et al. 1989). Another interesting physiological aspect of sage grouse is that they may face limits on energy production or protein metabolism caused by the need to detoxify sagebrush – limits on digestive rates of wildlife species have been suggested as important factors in metabolism (Karasov and Diamond 1985).

Sage grouse are extremely habitat specific, and one report states that "no other bird is so habitat specific to one particular plant type [sagebrush] in meeting annual life requirements" (Gunnison Basin Sage Grouse Conservation Plan, GBCP 1997, p. 38). The size of sagebrush habitat and lack of fragmentation of that habitat is crucial to the species because sage grouse species move seasonally to different areas within the sagebrush shrub-steppe (GBCP 1997, p. 38). Barriers to movement will cut the birds off from critical habitat. Sage grouse are unable to

adjust to patterns of land use that eliminate or adversely affect large tracts of sagebrush (GBCP 1997, p. 39).

Sage grouse provide a great deal of aesthetic enjoyment to bird watchers, recreationists, and hunters, and were relied on as a food source by many Native American tribes, who incorporated various rituals relating to the bird into their culture, including dances (Patterson 1952c, p. vii). The birds' renowned lekking behavior has occasioned a great deal of interest by behaviorists and evolutionary theorists, and the spectacular aural and visual displays of mating males have provided endless wonderment and amusement to the general public. The large number of publications in the popular literature testifies to the level of public interest in the species – recent examples include Fergus (2000) and Anonymous (2000b). Indeed, the species has even served as the inspiration for a Dixieland Jazz composition (Watters 1987).

Locomotion

Sage grouse are weak flyers and often prefer to walk to reach useable habitats except when snow cover increases their conspicuousness (GBCP 1997, p. 48; San Miguel Basin Conservation Plan, SMBCP 1998, p. 22). Especially for hens with broods, walking is the preferred means of locomotion (BLM 1999f). As BLM puts it: "roads, agricultural conversion, oil and gas development and seedings that do not result in the appropriate habitat in the appropriate place, all become barriers to grouse movement" (BLM 1999f). Sage grouse flight is slow, low, and laborious. Sage grouse spring into the air with some difficulty, particularly for the heavier bodied males (Johnsgard 1983). Less than half a minute is typically spent airborne – after 5 to 8 wing beats, sage grouse glide for 23 to 32 m, and then repeat this cycle (Girard 1937). The average distance covered during a flight bout is 575 m for males and 221 m for females (Girard 1937). Sage grouse are incapable of lengthy sustained flight – birds have been found dead in large reservoirs because of their inability to fly over them (Braun 1998a). Birds usually fly at heights of 14 m (females) and 23 m (males) (Girard 1937) but fly close to the ground when crossing ridges. This physiological performance explains the propensity for walking, and emphasizes the threat of habitat fragmentation to the bird.

Food Requirements

The importance of sagebrush in the diet of adult sage grouse is impossible to overestimate. However, it is incorrect to conclude that sage grouse can survive solely on sagebrush: forbs (wildflowers), insects, and probably grasses are both necessary and important for various life-history stages and at various times of the year.

Sage grouse lack a muscular gizzard and cannot grind and digest seeds: they must consume soft-tissue foods (Wallestad 1975a). This distinguishes sage grouse from many other grouse and related taxa, and limits them to the consumption of relatively soft food. Sage grouse possess an enlarged caecum, which functions to extract additional nutrients from the food, and depend on microbial digestion of cellulose (Leopold 1953).

Energy demand is likely greatest during the breeding season, during the pre-breeding season for females (during the period of egg production), and during winter. Besides male display (considered elsewhere in this review), a major source of energetic demand is thermoregulatory stress during winter. Energy demands increase when effective temperatures are below the lower critical temperature (T_{lc}), which is about –0.6 °C for winter acclimated birds

(Sherfy and Pekins 1994). Effective temperature is not the same as air temperature; rather, effective temperature is an index that seeks to integrate the thermal effects of air temperature, wind speed, and solar radiation. For example, a sage grouse exposed to air temperatures of 5 °C and moderate or high wind speeds might experience increased energetic demand even though the air temperature is above the T_{lc}. The construction of effective temperature indices are non-trivial, and laboratory, field, and modeling exercises and have not been conducted for sage grouse. Nonetheless, some physiological studies have been conducted on the effects of wind on sage grouse (Sherfy and Pekins 1995). These studies show that even relatively low wind speeds can substantially increase energetic demand at any air temperature below freezing. For example, even a relatively low wind speed of 2.7 m/s increases energetic demand by a factor of about 2.5 x the standard metabolic rate (SMR) of 0.6 ml O_2 g^{-1} hr^{-1}. This means that food requirements will increase substantially if adequate shelter from the wind cannot be found. Under some conditions, birds may be in immediate danger of hypothermia (i.e. they will die because they are unable to produce enough metabolism to stay warm in the cold, even when they have adequate food). Degradation of winter habitat can thus have strong effects on sage grouse. Even outside of winter, sage grouse select areas that minimize wind from both vegetation (Connelly, et al. 1994a, 1994b) and topographic features (Hupp 1987a, Hupp and Braun 1989).

Nutrition affects the productivity of all grouse and ptarmigans, and can be particularly important during the breeding season (Moss, et al. 1975). Females with better nutrition put more nutrients into eggs (Jenkins, et al. 1963), have larger clutch sizes and improved chick survival (Jenkins, et al. 1963; Eastman and Jenkins 1970). Nutrient deficiency is known to reduce egg and chick production in birds generally by reducing eggshell thickness (Gutowska and Parkhurst 1942, Taylor, et al. 1962; Ellis and Labisky 1966). More general reviews of the effects of nutrition of hens on offspring are given by Robbins (1983), King (1972), and the various publications by the Romanoffs – Romanoff (1934, 1960, 1967, 1972) and Romanoff and Romanoff (1949).

Nutritive issues are of extreme import to sage grouse declines because widespread habitat degradation severely affects nutrition, and hence productivity, throughout the species range. Food scarcity can affect energy intake, crude protein levels or amino acid balance, and intake of minerals and vitamins. Sage grouse diet and food availability presents interesting issues in nutritional ecology because the mechanism of resource depletion, cattle grazing, and associated "range treatments," differentially affects preferred food plants of sage grouse. This can easily lead to specific nutritional deficits, as well as general energy balance problems. These problems were previously thought unlikely in wild animals (King and Murphy (1985) but appear ubiquitous in sage grouse. I present a few examples of likely specific nutritional deficits below, but others may well exist in sage grouse.

Among minerals, deficiencies of calcium are more likely than are those of selenium or manganese because of organismal needs coupled with mineral availability in different portions of the continent (Robbins 1983). Other minerals are likely of intermediate availability relative to their requirements in sage grouse. Vitamin A is known to affect reproduction and growth in quail (Robbins 1983, p. 69). Vitamin A deficiencies can also have important but difficult to detect sub-lethal effects. For example, Vitamin A affects vision and hence predator detection and mortality rates. Vitamin A is not found in plants (Robbins 1983, p. 73), thus the spraying of pesticides in sage grouse habitat or grazing that sufficiently depletes food supplies or vegetation

structure needed for insect populations will also impact sage grouse. Vitamin C is known to be required in excess of organismal synthetic capacity in at least some game birds, especially during growth or when subjected to pesticides or other stress (Robbins 1983, p. 93). Vitamin C is also not as widespread in foodstuffs as other water-soluble vitamins.

Historically, clutch sizes as large as 26 eggs have been reported, but today clutch sizes average only 7 to 9 eggs (Schroeder 2000f). Although anecdotal, the historical reports are suggestive when contrasted with present day data. Also, annual variation in clutch size supports the hypothesis of nutrient limitation (Schroeder 2000f). Nutrient deficiencies are often reflected in reduced clutch size, reduced provisioning of each egg, and consequent poor survival and growth of young chicks. These are precisely the end effects suggested by Crawford and Gregg (2001) as one bottleneck affecting sage grouse in Oregon. The nutritional status of pre-laying hens is related to forb abundance and nutritive value, and decreases in average brood size tracks decreases in forb abundance (Barnett and Crawford 1994). Blood analyses show that female sage grouse in Oregon experience protein deficits during the pre-breeding season (Wagner, personal communication). This is likely due to inability to find adequate forbs and insects during this period. Effects on chicks are likely even more important. Chick survival appears to be related primarily to productivity of forbs and insects (Drut, et al. 1994b). It is likely that one major effect of habitat degradation by livestock grazing is that sage grouse are literally being starved across their range.

Sagebrush

Numerous studies have documented the year-round use of sagebrush by sage grouse (Beck 1975a, 1975b; Call 1979; Call and Maser 1985; Klebenow 1972; Patterson 1952c; Schneegas 1967; Sime 1991; Wallestad 1975a; Wallestad, et al. 1975). A Montana study, based on 299 crop samples, showed that 62 percent of total food volume over the year was sagebrush. Between December and February sagebrush was the only food item found in all crops. Only between June and September did sagebrush constitute less than 60 percent of the sage grouse diet (Wallestad 1975a). Sage grouse are incapable of digesting most seeds or other hard foods as they lack a muscular gizzard (Johnsgard 1983).

Sage grouse differentially choose certain sagebrush species, and this preference apparently relates to protein levels and monoterpene concentrations in different species (Remington and Braun 1985, Myers 1992). Sage grouse generally prefer big sagebrush to other species (Eberhardt and Hoffmannn 1991, Tirhi 1995). However, sage grouse in Antelope Valley, California, browsed black sagebrush more frequently than the more common big sagebrush (Schneegas 1967). Among the big sagebrush subspecies, basin big sagebrush is less nutritious and higher in terpenes than either mountain or Wyoming big sagebrush. Sage grouse prefer the other two subspecies to basin big sagebrush (Autenrieth, et al. 1982). Welch, et al. (1991) found that sage grouse preferred mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, in order from most preferred to least preferred. Remington and Braun (1985) found that Wyoming big sagebrush was preferred over mountain big sagebrush; however, their sagebrush samples were from different areas. Sage grouse will also eat other sagebrush species to a lesser extent than big sagebrush, including Alkali sagebrush (*A. longiloba*), black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*), and half shrub fringed sagebrush (*A. frigida*) (Barnett and Crawford 1994; Patterson 1952c; Remington and Braun 1985; Rogers 1964;Wallestad, et al. 1975).

During winter, sage grouse have been observed selecting plants with high protein levels (Remington and Braun 1985). Vegetation high in nitrogen is preferred by sage grouse (O. Myers 1992). Sage grouse require high quality foods in winter (Welch, et al. 1988).

Forbs

Apart from sagebrush, the adult sage grouse diet consists largely of herbaceous leaves, which are consumed primarily in late spring and summer. Sage grouse are highly selective consumers, choosing only a few plant genera. Dandelion (*Taraxacum* spp.), legumes (Fabaceae), yarrow (*Achillea* spp.) and wild lettuce (*Lactuca* spp.) account for most of their forb intake (Autenrieth, et al. 1982; Sime 1991). Tirhi (1995) lists salsify (*Tragopogon* spp.), and the legumes clover (*Trifolium* spp.) and milkvetch (*Astragalus* spp.) as important forbs in sage grouse diets. Martin (1970a) found that from July to September, dandelion comprised 45 percent of sage grouse intake; sagebrush comprised 34 percent. Collectively, dandelion, sagebrush, and two legume genera (*Trifolium* and *Astragalus*) contributed more than 90 percent of the sage grouse diet.

Forbs are critical for egg productivity and nutritional status of hens during the pre-laying period and are taken selectively over sagebrush (Barnett 1992, Barnett and Crawford 1994). Lack of forb availability during the pre-laying period reduces nest initiation rates and nutrient content of eggs (Crawford 2000c). Sagebrush is a negligible constituent (1%) of the diet for young sage grouse up to 11 weeks of age (Peterson 1970b, Pyrah 1971). Instead, forbs constitute more than 50% of juvenile diets up to 11 weeks of age (Klebenow and Gray 1968, Peterson 1970b). Lack of forbs and insects reduces the nutritional condition of chicks that do hatch and reduces recruitment of juveniles into the fall population (Crawford 2000c). This occurs even when sagebrush is still available (Crawford 2000c). Forbs density has been "greatly diminished by a long-term history of livestock grazing and invasive competitors" (Altman and Holmes 2000, p. 25).

Insects

Overall, insects are a minor diet item for adult sage grouse but are nonetheless necessary and extremely important dietary components depending upon seasonality and life history stage. Martin, Zim, and Nelson (1951) reported that insects comprised 2 percent of the adult sage grouse diet in spring and fall and 9 percent in summer. Sagebrush made up 71 percent of the year-round diet. Females are known to consume cicadas (Sime 1991, p. 27). It is likely that gravid females have increased nutrient demands (Robbins 1983), and may require increased amounts of micro-nutrients, protein, and lipids. Gates (1983, p. 63) found that hens used forbs most both before and after incubation. Also, high density foods such as insects have a disproportionate amount of nutrients relative to their proportion of dietary composition. Some insects are obligates on certain kinds of sagebrush and some specialize on certain leaf types (Winward 1991a). The degree to which sage grouse may specialize on various insect species or morphs is unknown.

Insects are a necessary food item for sage grouse chicks. In their first week of life, sage grouse chicks consume primarily insects, especially ants and beetles (Patterson 1952c). Insects can constitute up to 75% of the diet of juvenile sage grouse (Patterson 1952c). Survival and growth rates of chicks decrease proportionately with decreased insect material in the diet, even when diets contained abundant preferred plant material (Johnson and Boyce 1990).

Older chicks switch to forbs, with sagebrush gradually assuming primary importance. In a Utah study, forbs composed 54 to 60 percent of the summer diet of juvenile sage grouse, while the diet of adult birds was 39 to 47 percent forbs (Trueblood 1954). Martin (1976) found that the diet of juveniles was 76% plant material, 24% animal. Common dandelion and common salsify were the two most important plant items in the diet, occurring in 55 and 63 percent, respectively, of the 127 crops analyzed.

Even as adults, sage grouse do not eat an entirely plant based diet. Patterson (1952c) found that sagebrush constituted 77% of the diet, and plant materials overall constituted 95.7% of the diet. Though small, the remainder may nonetheless be important for micronutrients or particular amino acid constituents. Martin, et al. (1951) reported that sagebrush composed 71% of the adult diet, and that animal material ranged from 9% in summer, to 2% in spring and fall. Only between June and September does sagebrush constitute less than 60% of the diet (Wallestad 1975a). Animal material in the adult diet could be crucial for proper nutrition because it may serve as a vital source of particular amino acids or micro-nutrients. Rodriguez (1988) suggested that sage grouse select sagebrush on the basis of micronutrient content.

Water Requirements

Sage grouse apparently do not require open water for day to day survival if succulent vegetation is available. They will use free water if it is located in meadow vegetation (Savage 1968). Hens with broods avoid water surrounded by bare ground, such as areas trampled by livestock (Klebenow 1982). In some areas, sage grouse distribution may be seasonally limited by moisture gradients as expressed in riparian vegetation. In summer, sage grouse in true desert regions occur only near streams, springs, and water holes (Howard 1996). However, this may be due to dependence on succulent vegetation rather than on any need for free water. Physiological studies of water conserving ability and osmoregulatory function have apparently not been conducted.

In winter in Eden Valley, Wyoming, sage grouse have been observed visiting partially frozen streams to drink from holes in the ice (Call 1979). Sage grouse have been observed frequenting wet meadows and riparian areas in some studies (Pederson 1982; Willis, et al. 1993) but not in others (Cadwell, et al. 1994). Water has been considered a key component of summer and fall habitat by some (Carr 1967a, 1967b; Savage 1969a; Call and Maser 1985) but this may be merely an epiphenomenon of more succulent vegetation occurring near water, as others have not found that sage grouse prefer sites close to open water (Wallestad 1975a; Autenrieth 1981; Cadwell, et al. 1994). Without samples of vegetation water content, this issue is unlikely to be resolved – moreover, spatial analysis of habitat degradation and conversion is a substantially higher research priority. It is important to exclude cattle from wet meadow areas (Jones and Braun 1994).

Because there were far more sage grouse before the period of Euro-American settlement of the West than are extant currently, there is no reason to suppose that water developments associated with livestock operations provide any net benefit to sage grouse (Schroeder, et al. 1999a, p. 16). Indeed, water "catchments or guzzlers have not been shown to benefit sage grouse populations" (Braun 1998c, p. 4). Instead, such water developments lower water tables and channel water away from succulent vegetation areas such as wet meadows that sage grouse do require. Another negative impact is that such developments may serve to concentrate sage

grouse, increasing the likelihood of disease transmission (Schroeder, et al. 1999a, p. 17). Sage grouse do not require free water and do not benefit from guzzlers, water tanks, stock ponds, or other water sources independent of riparian vegetation (Braun 2001e).

Demographics and Life History Events

Sage grouse are long lived birds (BLM 1999c) and may live up to 10 years in the wild (Dalke, et al. 1963; Wallestad 1975a; Tirhi 1995, citing Braun, personal communication), but a more common lifespan is probably 2 to 3 years (Wallestad 1975a). However, 4 and 5 year old birds are not unusual (BLM 1999c). Elman (1974) found average life spans of only 1 to 1.5 years, while Drut (1993) indicated that a typical lifespan was 2 to 4 years. Returns of marked birds returning to the strutting grounds one year later ranged from 5% to 21% over a 3 year study (Dalke, et al. 1963). Annual mortality rates have been reported as 50% to 60% in two studies (Braun 1975, Tirhi 1995, citing Connelly, personal communication). However, Schroeder (1994a, 1994b) reported annual mortality rates of 29%. The Service reported annual mortality rates of 50% to 55% (FWS 2001d, 66 Fed. Reg. 22984, 22985).

Sex ratios, determined mainly from hunting data, typically range from 1:1 (Girard 1937) to 1.5 (Rogers 1964) for all sage grouse age classes. For juveniles, sex ratios were reported as 1:1.1 in Colorado (Braun 1984) and 1:1.2 and 1:2.3 in Wyoming (Patterson 1952c). Braun also reported sex ratios of 1:1.6 for yearlings and 1:2.6 for adults. Most of these reported sex ratios do not support the 1:2 male to female ratio assumed in the various conservation agreements for the Gunnison sage grouse (see below). In Colorado and Wyoming, populations were composed of 51% and 58% juvenile birds, respectively (Patterson 1952c, Rogers 1964). Sex ratios in both states were about 40% males.

Different stressors act at different seasons on different age classes and sexes. Breeding and nesting periods are energetically demanding: sage grouse experience a negative energy balance at these times and lose weight (Beck and Braun 1978).

Poor nesting success and mortality of young chicks are the most common factors acting to reduce population size and prevent population increase (Braun 1999a, p. 1). In some years, over-winter mortality is most limiting (Braun 1999a, p. 1).

Lekking

Leks are traditionally used sexual display grounds where males concentrate and cluster spatially (Beehler and Foster 1988) allowing females to observe large numbers of male displays, and exercise mate choice. The term was apparently first used by Selous (1906-1907). Leks are usually located in areas where females travel between wintering and nesting areas (Gibson 1996b). Males on leks utter unusual vocalizations (Welch, et al. 1995) and engage in visual displays that are "one of the most complex stereotyped motor patterns found among birds" (Wiley 1973b). The vocalizations apparently serve to attract females (Gibson 1989), as do the visual displays. Male mating success is correlated with display rate (Gibson, et al. 1991). Leks can range in area from 0.04 to 40 hectares and from several males to about 50 males; however, leks contained much larger numbers of males historically – accounts suggest 400 or more males at single leks (Scott 1942; Call 1979; Call and Maser 1985; Trimble 1989, p. 104). There appears to be a minimum viable number of males for a lek – there are numerous reports of leks being abandoned and apparently coalescing into a smaller number of larger leks (see, e.g. the

Washington Population Assessment section). This is consistent with contemporary theories of female choice and supra-stimuli displays for mating (see the numerous papers by Gibson and by Wiley in the Bibliography), but also points up the danger of assuming that lek use will continue as population level decline. Males seek lekking areas with high quality habitat, and with large numbers of males and females present (Bradbury, et al. 1989a). Thus, as the number of individuals at a lek becomes smaller, it will eventually be abandoned at some threshold size. Such factors will contribute to Allee effects in sage grouse.

Males gather on the lek in late February to April, as soon as the lek area is relatively free of snow. Yearling males arrive somewhat later (Eng 1963, Rothenmaier 1979). Sage grouse are highly conservative in moving to new leks, and in retaining use of traditional leks. Only a few dominant males, often only two, breed. Females typically gather on the lek beginning in mid-March, although this varies with weather conditions. Sage grouse mating behaviors, which are complex, are summarized by Johnsgard (1973). Older males establish lek territories earlier than younger males and exclude the latter; males with territories near the center of a lek have higher mating success (Davis 1978). Thus, younger males have significantly reduced mating success. Males employ vocalizations and visual displays that attract females and either repel or antagonize other males (Hjorth 1970, Hartzler and Jenni 1988). All adult males repel subadult males from leks (Thorvilson 1969).

Auditory elements of the display are generated by the rapid inflation and especially deflation of the ventral air sacs, and possibly by wing movements. Dr. Clait Braun noted that the auditory display of the Northern sage grouse sounds like the a "poik, poik." This vocalization is apparently the result of 2 pops of the air sac in the Northern species (J. R. Young, et al. 1994). Males employ 16 or more elements in the strutting sequence (Welch, et al. 1995). Displays typically occur at dawn and dusk (Dalke, et al. 1963; Johnsgard 1973; Wallestad and Schladweiler 1974); however, on cloudy days, displays continue through the middle of the day. Thus, exclusion of humans from lek areas only at dawn and dusk will not offer adequate protection of the lek area.

Males deplete lipid reserves during courtship, indicating that lekking activities are energetically demanding for them (Hupp and Braun 1989a). The holding of center territories entails even more energetic demand (Beck and Braun 1978). The cost of display in males is often 13.9 to 17.4 times BMR, basal metabolic rate (Vehrencamp, et al. 1989). Male display is thus an extremely demanding activity, far exceeding the instantaneous power demands of thermoregulation, and nearing or exceeding the 8x to 15x BMR of flight (Rayner 1982, Webb 1990). Moreover, lipid reserves are influenced by winter snowfall and air temperature (Hupp and Braun 1989a), showing that exposure caused by inadequate winter habitat cover or winter food could affect breeding activities, and hence fitness and population persistence, even if the effect was too small to affect individual survival.

Of particular importance for the analysis of population viability is that a very small proportion of males obtain nearly all matings – typically, only 1 or 2 males per lek (Scott 1942; Patterson 1952c; Lumsden 1968; Hjorth 1970; Johnsgard 1973; J. R. Young 1994b, p. 33). Thus, effective population sizes (N_e) are significantly smaller than actual population sizes, and consequently, the effects of genetic stochasticity and demographic stochasticity are highly magnified in these birds. Older, established males are known to repel subadults from leks (Thorvilson 1969, p. 2). Copulations outside of the very small "territories" (0.01 hectare)

defended by males are often interrupted by other males, usually before sperm transfer is effected (Gibson and Bradbury 1986, p. 385). Thus, counting of copulations per se may overpredict mating success. Even if copulations are obtained by younger males (which often lack central lek "territories") they are likely to be ineffective.

Another effect on extinction dynamics is caused by the lekking habit. Hoglund (1996) suggested that lekking affects both distribution and local extinction risk.

Pre-Laying Period

During the period before a hen lays her clutch (and possibly including much of the lekking period), protein balance is critical for successful reproduction by hens. Hens require a diet with at least 18% crude protein (J. Craig, personal communication). However, sagebrush provides only 14-16% crude protein, so a diet rich in forbs is crucial (Barnett and Crawford 1994; J. Craig, personal communication). Forbs are also higher in calcium and phosphorus than is sagebrush (Barnett and Crawford 1994). Forbs contribute 20% to 50% of the diet for pre-laying hens, and lack of forbs in the diet will cause reductions in the number of eggs and fledglings (Barnett and Crawford 1994). Nutritional status in female sage grouse is known to reduce reproductive success (Barnett and Crawford 1994). It is also well established in related species that chick survival is related to the physiological condition of the female before laying (Moss, et al. 1975; Riley, et al. 1998; Eastman and Jenkins 1970; Hudson, et al. 1994).

Egg formation and nesting are known to be energetically demanding periods for female sage grouse (Beck and Braun 1978). The same is true for many, and perhaps most, other species of birds (King 1972, 1974; Robbins 1983). Thus, females likely accumulate fat stores during winter and the lekking season to last throughout the breeding season. If they are unable to do so, or if they must squander these energetic resources in long distance movements, breeding will fail. Likewise, if habitat near the lek is not suitable for nesting, then females must move long distances. This effect has been noted in studies by Autenrieth (1981) and Crawford, et al. (2000). Such long distance movements deplete energy and nutritive reserves and expose females to predation.

Nesting

Nest success is usually cited as the main factor affecting population dynamics of sage grouse (summarized in Schroeder, et al. 1999a, p. 15). Nest success is strongly influenced by habitat characteristics, such as tall and thick grass and forb cover in sagebrush shrub. There are "substantial" data "correlating rates of nest success" with these habitat characteristics (Schroeder 2001a, 2000f, summarizing numerous studies). Grazing and fire strongly influence these vegetative characteristics. Survival of juveniles and adult over-winter survival are also frequently cited as perilous life history stages for sage grouse. However, little has been done to manage habitat for any of these life history stages. Consequently, populations have plummeted throughout the West.

After mating, the hen leaves the lek for the nesting grounds. The hen builds a nest, which is concealed under sagebrush and in grass and forb cover (Jarvis 1974). Shrubs as well as forb and grass cover are essential components of quality nesting habitat (Sveum 1995). The nest is a shallow depression slightly lined with grass, twigs, or sage leaves (Girard 1937, Rasmussen and Griner 1938, O. C. Nelson 1955, Autenrieth 1981). Standard guides provide comparative

information, as well as color photographs and drawings of nests, eggs, and chicks (Ehrlich, et al. 1988; Harrison 1978; Harrison 1979).

Laying occurs 7 to 10 days after mating (Petersen 1980b, Autenrieth 1981). Yearling females lay later than do adults (Petersen 1980b). Hens typically lay 1 egg per 1 to 2 days (Petersen 1980b, Johnsgard 1983). Hornaday listed the clutch size as 13 to 17 (Hornaday 1916, p. 193; Willett 1906; Patterson 1952c). Modern accounts give clutch sizes averaging 7 to 8 eggs, ranging from 6 to 13 eggs (O. C. Nelson 1955; Autenrieth 1981; Johnsgard 1973, 1983; Schroeder 2000f). This suggests that sage grouse may now be experiencing reduced clutch sizes, probably due to poor nutrition of females caused by habitat degradation. Schroeder, et al. (1999a) suggested that these historically larger clutches might have been the result of egg dumping; however, brood parasitism has never been noted in sage grouse, and the lower clutch sizes now commonly seen may be a result of the widespread habitat degradation found throughout the range.

Incubation time is 25 to 27 days (Harrison 1978). An incubation time of 27 to 28 days is listed for the Gunnison sage grouse (GBCP 1997, p. 3). Eggs are olive, yellowish, or greenish, and finely dotted with brown tones. They are oblong and about 2.2" (55 mm) in diameter (Ehrlich, et al. 1988; Harrison 1978; Harrison 1979).

Males do not participate in nesting, incubation, or brooding (Wallestad 1975a, Autenrieth 1981). Consequently, the female must leave the nest unattended to forage. O. C. Nelson (1955) and Girard (1937) reported that excursions off the nest last about 15 to 25 minutes, about twice a day during incubation. Girard (1937) reported that excursions from the nest were bimodal, occurring from about 9:30 to 11:30 am, and from 2:00 to 3:00 pm. Such excursions are consistent with biophysical analyses indicating that shading of the eggs from radiative exposure during the middle of the day is necessary (Webb 1993a, 1993b). The timing of nest absences to late morning and early afternoon is consistent with temporal periods of hypothermic environments early and late in the day, as found by Webb and King (1983a) for other species.

Reduced forb and grass cover near the nest negatively impacts the nest microclimate (Autenrieth 1981, Call and Maser 1985, Webb 1993b). The amount of grass cover over 18 cm. in height near the nest differentiates successful from unsuccessful nests (Gregg 1992; Gregg, et al. 1994). Call (1979) developed management recommendations for sage grouse habitat, and a series of recommendations and guidelines have been issued by the Western States Sage Grouse Technical Committee (WSSGTC 1999). As discussed elsewhere in this review, however, the WSSGTC guidelines are incomplete.

Nest productivity is very low in sage grouse. A substantial proportion of birds do not attempt to nest, and of the ones that do, hatch rates are low. Consequently, "it takes sage grouse longer to rebound from low population levels than any other game bird" in Idaho (Eustace 1995 quoting J. Connelly, personal communication).

Sage grouse have high rates of nest desertion and nest predation (Gregg, et al. 1994; Johnsgard 1973). Summarizing data from several sage grouse studies, Gill (1966b) found a range of nesting success from 23.7 to 60.3 percent, with known predation accounting for 26% to 76% of lost nests, and averaging 47.4% across the 503 nests in the summary. Bergerud (1988c) also reviewed this literature and found nesting success to average 35% in 699 nests over 12 studies, with the predation rate averaging 50%. This is the lowest nesting success in any grouse reviewed by Bergerud and the highest predation rates (Bergerud 1988b, p. 593, Table 15.2 and p.

601, Fig. 15.10). In Idaho, supposedly a stronghold of sage grouse, nesting success is even lower (44%) (Apa 1998). Bergerud (1988b) also found sage grouse to have the greatest reduction in nesting success of yearlings relative to adults of any grouse reviewed. Sage grouse are not determined nesters (GBCP 1997, p. 3). Sage grouse are known to readily abandon nesting attempts when disturbed. Disturbances need not be in close proximity to the nest. For example, one radio-marked hen abandoned her nest when a fencing crew was working on a fence 300 yards away, even though the nest was within two or three days of hatching (Eustace 1995, p. 26 citing J. Connelly, personal communication).

The primary cause of nest loss is predation (DeLong, et al. 1995). Sage grouse nests experience significantly higher predation when more densely spaced (Niemuth 1992, Niemuth and Boyce 1995). Thus, habitat fragmentation, degradation, or conversion, which concentrates nesting females into smaller areas, will cause higher mortality at this critical time in the life history.

Renesting is low in sage grouse (Connelly, et al. 1993, p. 1042; Hanf, et al. 1994) and may be further inhibited by moisture and vegetation conditions (GBCP 1997, p. 3). Renesting may be limited by male reproductive condition (Eng 1963). Of the hens losing their nests, only 15% will renest (BLM 1999c). Subsequent nests, if attempted at all, have few eggs and reduced success (Hulet 1983). Clutch sizes of second nestings are reported to be only 4 to 7 eggs (GBCP 1997, p. 3). These findings point out the importance of preventing disturbance to nesting sage grouse. Bergerud (1988b) also reviewed two studies on renesting rates in sage grouse, finding it to average 42%. Other studies have found renesting rates to be about 10% (Patterson 1952c, Autenrieth 1981). Finally, Bergerud (1988b, p. 606, Fig. 15.13) found that higher densities of males were related to lower juveniles per adult in sage grouse. This effect has conservation implications: as birds are crowded into smaller and smaller habitat fragments, population productivity can be expected to decline.

Brooding

Females typically produce only a single brood per year. Development is precocial, and the chicks are mobile and down covered (Patterson 1952c). The female tends the young and shows them food and foraging sites. Hens cover chicks to protect them from severe weather and use frequent vocalizations for contact enhancement (Girard 1937, Patterson 1952c).

Chicks fly by 2 weeks of age, although their movements are limited until they are 2 to 3 weeks old (Wallestad 1975a). They can sustain flight by 5 to 6 weeks of age. Juveniles are relatively independent by the time they have completed their first molt at 10 to 12 weeks of age (Girard 1937, Patterson 1952c, Johnsgard 1983). The hen and her chicks mix with other sage grouse on the summer ranges (Patterson 1952c).

Juvenile mortality is high in sage grouse, and most juvenile mortality takes place in the first 2 weeks after hatching, before the chicks are able to fly (Patterson 1952c, Autenrieth 1981). Some studies have found that most chick mortality takes place in the first 4 weeks of life (Coggins 1998). During the pre-flight period, chicks respond to predators by freezing – their cryptic coloration provides good pattern matching, so long as adequate vegetation is available for cover (Patterson 1952c). The major predators on chicks are corvids, raptors, and various mammals (Autenrieth 1981, Presnall and Wood 1953). Ready availability of food and cover is crucial to juvenile survival (Klebenow 1972, 1985). Hickey (1955) reported early brood

mortality ranging from 32% to 54% in three studies. Ricklefs (1969) has analyzed the significance of high egg and juvenile mortality in a population and evolutionary context. Bergerud (1988b, p. 618, Table 15.6) reviewed mortality rates for various grouse species and found that nest mortality rates for sage grouse were 59%, and chick mortality rates were 29%, with mortality rates of adult females being 37%. Other reports of chick mortality rates range from 40% to over 60% (Wallestad 1975a, Braun 1975). Mortality of chicks caused by wet weather during the brood-rearing period is not sufficient to account for population size during the following year (Jenkins, et al. 1967; Bergerud 1970; Bendell 1972a, 1972b; Myrberget 1972; Watson and Moss 1979 in Rich 1985a).

During the first week of life, chicks may be obligate insectivores (Klebenow and Gray 1968, Johnson and Boyce 1990, 1991), and depend on ants, weevils, and beetles, later adding grasshoppers to the diet (Patterson 1952c). Drut, et al. (1994b) identified three families of insects as major sources of food for young chicks: Scarabaeidae, Tenebrionidae, and Formicidae. Where insects and forbs are depleted, sage grouse survivorship will decline: in an area with higher grouse productivity, forbs and invertebrates composed 80% of dietary mass; however, in an area with lower productivity, chicks consumed primarily (65%) sagebrush (Drut, et al. 1994b).

As the chick grows, the proportion of insects in the diet steadily drops, being about 75% in the first few weeks, to about 10% in the later part of the juvenile period. Forbs constitute a high proportion of the diet for juveniles (Klebenow and Gray 1968). Trueblood (1954) reported that juveniles strongly preferred forbs and showed an aversion to grasses. Although sage grouse are found in alfalfa fields, they apparently seek out dandelion and salsify which are readily available in alfalfa fields (Peterson 1970b). Late in summer, as forbs become less available, juveniles shift to sagebrush and fringed sagewort (*Artemisia frigida*). The latter, a relative of sagebrush, may constitute a transitional food for juveniles (Peterson 1970b). The observation of sage grouse in alfalfa and other agricultural fields results from several factors: they are easier to see in alfalfa than in sagebrush areas, the richest natural foraging habitats have been converted into alfalfa fields leaving the birds nowhere else to go, and alfalfa is fairly nutritious and will be eaten so long as the birds are not too far from sagebrush cover for predator escape. That habitat conversion to alfalfa fields is not good for sage grouse follows from the obvious result that as large areas have been converted to alfalfa, sage grouse numbers have declined, not increased.

Martin (1970a) found that sage grouse diets during summer were composed of 34% sagebrush, and 45% dandelion (*Taraxacum* spp.). Together with forbs from two other genera (*Trifolium* and *Astralagalus*) these constituents totaled 90% of the diet. Other studies have also found forbs to be important dietary components (Leach and Hensley 1954, Leach and Browning 1958). Other highly used forbs during spring and summer include clover (*Trifolium* spp.), salsify (*Tragopogon* spp.), milkvetch (*Astragalus* spp.), and prickly lettuce (*Lactuca* spp.) (Peterson 1970b, Pyrah 1971, Johnsgard 1983).

Summer & Autumn

In late summer, Girard (1937) reported that sage grouse roost until about 6:00 am, forage until about 10:00 am, rest during the middle of the day, forage again from about 3:00 pm to 8:00 pm, and roost at about 9:00 pm.

Males and hens without broods, which typically form small gender-based flocks in the spring, move to summer ranges in the following order: males, broodless hens, and last, hens with broods (Schoenberg 1982; Connelly, et al. 1988). Young males typically flock with females that are segregated from male flocks (Patterson 1952c, Dalke, et al. 1960; Dunn and Braun 1986a). Movements to wintering areas are initiated by decreases in temperature and reductions in forb availability (Patterson 1952c; Dalke, et al. 1963). Female habitat selection and movement patterns are directly linked to forb cover (Gregg, et al. 1993) which in turn is determined by livestock grazing, recovery from strip mining, and other threats. Generally, populations will decline if the number of chicks produced by each hen is less than about 2.3 in the autumn (Nevada State Office, BLM 2000a, p. 3, citing Connelly and Braun 1997, Edelmann, et al. 1998; Compton and Connelly, unpubl. data).

Over-wintering

Sage grouse form unisexual winter flocks (with immature males associating with females). In the past, these flocks sometimes ranged upwards of 1,000 birds during severe weather, while in more moderate weather flocks typically ranged from 50 to 300 birds (Dalke, et al. 1963). In winter, birds do not migrate long distances, and survival over winter depends on adequate cover and food. Grouse have little metabolic resistance to winter fasting and must feed regularly to maintain energy balance (Thomas 1987). Sagebrush is consumed almost exclusively during winter, and also provides cover for the birds from the very high wind speeds common in their winter range. Of particular concern is that the birds must not only survive the winter but also need to emerge from the winter season with sufficient lipid stores for male mating displays (Hupp and Braun 1989a; King 1972) and perhaps for female egg production (King 1972, Robbins 1983). Older birds carry larger lipid stores than do yearlings (Remington and Braun 1988), reinforcing the conclusion that yearlings are less likely to mate and breed successfully. Bergerud (1988a) suggested that the reason that not all sage grouse females ovulate and nest was because of yearling females in the population. This is consistent with physiological limits from overwintering stress, but could also result from inexperience, or delayed maturation.

Sage grouse show some site fidelity to wintering areas. Berry and Eng (1985) observed hens in Montana moving to known wintering areas before the onset of heavy snowfall, suggesting fidelity to specific wintering areas. Thus, sage grouse will be particularly susceptible to destruction or degradation of traditional wintering areas. Winters also fluctuate in severity. For example, Dr. Braun has stated that a severe winter will occur at 7 to 10 year intervals in North Park, Colo. (Summary of North Park Working Group Meeting 1999, p. 5). Even with operation of the proposed conservation plans, such winters would "certainly [cause] decreases in population" (id., p. 6). Even if birds are not directly killed during a winter, severe winters are known to alter lek behavior (Gibson and Bradbury 1987).

Seasonal Movements

Sage grouse often move from summering to wintering areas seasonally, although the movement distances vary dramatically depending upon the distances between areas of adequate quality habitat, weather, and other factors (Connelly, et al. 1988), perhaps including knowledge of habitat areas by experienced individuals in the population. Intermittent stream drainages are often used as migration routes (Hupp 1987a; Lyon 2000, p. 5). Some groups of sage grouse

move substantial distances among nesting, lekking, brooding, and wintering areas, while others are nearly sedentary, perhaps because of loss of habitat corridors. Additionally, some lowland wintering areas may not be used at all until years of severe weather (Stiver, personal communication, 2000), increasing the likelihood of sharp population decreases in years with severe winters, even when populations may appear healthy.

Sage grouse occupying low elevation areas often do not migrate (Wallestad 1975a). Of the populations that do migrate, movements are typically on the order of a few dozen kilometers or less. Longer movements have been reported, but there is no doubt a bias to report such extreme events, as neither journals nor individual scientists consider typical movements of much note. Patterson (1952c) summarized the early literature on seasonal movements. Seasonal movements are often somewhat greater than 16 km (Berry and Eng 1985). Within the wintering range, Colorado sage grouse moved an average of 1.5 km per day, then dispersed an average of 27 km to the spring leks (Schoenberg 1982, p. 24). Longer distance movements, ranging from 80 to 160 km have also been reported anecdotally (Pyrah 1954, Connelly and Markhamer 1983, Berry and Eng 1985). Much shorter distance movements are more common (Bradbury, et al. 1989a).

Fall movements to wintering areas are driven by weather conditions and usually occur gradually. After late winter or spring lekking activity, sage grouse may move to higher elevations or down to irrigated valleys for nesting and feeding. Most broods moved only a few km from nesting areas to summer ranges, but a few moved up to 13.4 km (Gates 1983). In contrast, movements from summering areas to wintering areas may be 50 km in Colorado, Wyoming, Idaho and Montana (Dalke, et al. 1960; Martin 1976; Beck 1977; Connelly, et al. 1988). Sage grouse may move only short distances, not at all, or distances in excess of 75 km between wintering, breeding, and summer ranges (Dalke, et al. 1963; Braun, et al. 1977; Connelly, et al. 1988; Fischer, et al. 1993a). These long distance movements may well be a response to habitat fragmentation in modern times.

A closer examination of these disparate movement distances is required. Schlatterer (1960) reported that in southern Idaho, brooding grounds were 13 to 27 miles (21-43 km) from the nesting grounds (see also Hulet, et al. 1986). In the Gates (1983) study, most males remained within 1.5 km of leks and only a few ventured as far away as 9 km, even though seasonal movements by flocks ranged up to 13.4 km. Movements by males probably have greater import for gene flow and sub-population cohesion because seasonal movements may merely represent flocks moving to different use areas and then back to familiar lek sites for breeding rather than interchange among different lek complexes.

Anecdotal evidence suggests that males may be capable of moving long distances over the seasons. During winter in Wyoming, Patterson (1952c) recovered a male sage grouse 75 air miles (120 km) from where he had banded it the previous summer. However, it is not known if the captured male moved purposefully, or was merely blown off course by the very strong winds common in Wyoming winters. Yearling males are much more likely to move long distances than are adult males, and some of the movements reported in the literature are the result of destruction of sagebrush by chemical sprays (Wallestad and Schladweiler 1974, Wallestad 1975b, Martin 1976). The Gunnison Basin Sage Grouse Conservation Plan reported movements by both sexes exceeding 20 miles to locate foraging and roosting areas (GBCP 1997, p. 5). No data support such long distance movements by adults outside of the winter season. Moreover, the movements

that did occur by Gunnison sage grouse and by grouse in Washington are likely extreme responses to the very low availability of habitat in those areas. Radio telemetry data indicate that males typically stay within 1.5 km of leks, although a few males were located up to 9 km away (Gates 1983). Movements from wintering areas to leks in the Gunnison Basin generally followed river valleys, and did not exceed 35 km even after a severe winter (Hupp 1987b, p. 62). After the breeding season, males in the Gunnison Basin remained within a few km of leks, and females remained within a few km of their nest sites throughout the summer (Hupp 1987b, p. 67).

Although limited, the best available scientific data indicate that birds typically move relatively short distances unless forced to move greater distances due to habitat limitations. Typical movements are only a few km, substantially shorter than the few anecdotal reports of long distance movements, and the latter may have been made by young birds. In some isolated areas, birds may habitually engage in longer distance movements. It is likely that mortality risk increases substantially as movement distances increase. Crawford reports that birds in Oregon may move up to 100 km but suggested this may occur because of vast expanses of severely degraded habitat (John Crawford, personal communication, March 14, 2000). Long distance movements may well be a response to extremely low food productivity in recent decades. For example, net primary productivity of grasses and forbs in some stands has fallen from 800 pounds/acre to only 100 pounds/acre (Winward 1991a). Moreover, once birds undertake a long distance movement from one seasonal area to another, smaller scale vegetation factors may determine within patch movements, which are often made by walking (John Crawford, personal communication, March 14, 2000).

It is important to distinguish seasonal movements by flocks of birds from movements between demes by individuals, and to distinguish both those movement patterns from movements between feeding, breeding, and roosting areas within the home range (Wallestad 1971). In analyzing movement data to assess gene flow and hence population size, what is important is not whether birds can move long distances, but whether birds do move long distances and breed sufficiently frequently for gene flow to overcome drift and other deleterious genetic and demographic aspects of small population size. For example, one female moved 106 air miles among different nesting, summering and wintering areas, but then nested within 25 meters of her previous nest (Hulet, et al. 1986). Such long distance movements, coupled with lek and site tenacity, must not be confused with dispersal and subsequent gene flow. Dispersing individuals must successfully find appropriate habitat conditions and a mate, be sexually mature and active, be able to merge into the existing social structure, and successfully breed and raise those offspring to breeding status (Wiens 1976, p. 89). Dalke, et al. (1963) noted that movements of birds between leks were rare, both within a single season, and from year to year. Movements of males among leks ranged from 500m up to only 4.3 miles, and appeared to involve subordinate, rather than dominant males (Dalke, et al. 1963). Gibson and Bradbury (1986) note that movements among leks by yearlings are common, while movements by older males are merely "occasional." Yearlings are least likely to obtain matings. The data on older birds includes second year males and all non-yearlings, but since only 1 or 2 of the most experienced birds obtain nearly all matings at a lek, using inter-lek movement data will over-predict gene flow. Thus, gene flow among leks, and especially among different complexes of leks will be quite low.

Very large movements by sage grouse require the protection of vast amounts of acreage. In contradistinction, where sage grouse are relatively sedentary, gene flow among demes is reduced, increasing extinction risk.

Summary of Life History and Habitat Needs

J. R. Young (1994, p. 44) suggested that two habitats and life history periods critically limited Gunnison sage grouse: the density and height of sagebrush in winter, and the abundance of forbs and grasses in the summer early or late brooding periods. Braun (personal communication) feels that no specific life history stage or habitat type used is limiting across the entire range, and, instead, that certain habitat types will be limiting in certain areas, and others in other areas. When fluctuations in rainfall, snow pack and other variables are added, this would lead to a very complex landscape management prescription.

Even individual sage grouse need habitat blocks sufficiently large that they can stay 1.4 km from any trees (J. R. Young 1994b, p. 45, citing Schneider and Braun 1991). This means that any habitat smaller than about 3 km across is essentially unusable by sage grouse if the edges are defined by trees, poles or other suitable raptor perches.

Population Mechanisms & Vulnerability

Sage grouse possess certain physiological, anatomical, behavioral and population characteristics that render them more vulnerable to various environmental effects in terms of extinction risk. A variety of studies have identified increased vulnerability to extinction due to the following factors: small population size, low population density, isolation of sub-populations (demes), ineffectiveness of dispersal, large body size, large home range size, concentration of individuals (e.g. lekking), non-random mating system, and low fecundity, among others (Ehrenfeld 1970; Terborgh 1975, 1976; Pimm, et al. 1988; Primack 1993). These characteristics and the others discussed throughout this review constitute threats to the species within the purview of the ESA.

One such characteristic is large body size. Sage grouse are the largest grouse in North America, and large body size increases metabolic rate and food requirements. Space needs, such as foraging area, are increased as a consequence. Sage grouse are diet and habitat specialists, and this high dependence on particular habitat and food types increases the likelihood of extinction should those habitats become degraded.

Additionally, the "principal demographic properties contributing to" status as a "threatened or endangered species" are "a low maximum breeding population size and a high coefficient of variation in that size" (Ehrlich and Wilson 1991, citing Pimm, et al. 1988).

An important concern is that extinction probabilities among birds are more closely related to population density than to the area occupied (Bolger, et al. 1991). This is of particular importance to sage grouse, which range across large areas, but are extremely sparsely distributed across those areas. Moreover, Pimm, et al. (1988) showed that extinction risk was correlated with variation in population size – another significant concern for a species such as this, which often fluctuates in population size. These problems are exacerbated by the low intrinsic rate of increase in sage grouse, which also results in higher extinction risk (Pimm, et al. 1988, p. 760). Although the range of the species is large, it has been greatly reduced. Soule (1983) found that such range reductions are the time at which conservation efforts should be concentrated, as

species may be inevitably doomed in the periods of decline following range reductions. Sage grouse posses many of the biological traits that are known to increase extinction risk based on both ecological and paleontological studies: a specialized diet, low fecundity, relatively long lifespan within its taxon, complex behavior, low mean abundance, and high variation in abundance (McKinney 1997, Table 1, p. 499)

The lekking habit can also enhance the spread of disease and parasites because it concentrates large numbers of birds in small areas. The fact that lekking reoccurs in the same areas year after year permits disease organisms, vectors, and parasites to easily reinfect birds if they can over-winter in a cyst, egg, or other resting stage. Sage grouse are restricted to particular types of nest sites, thus increasing their susceptibility to degradation or destruction of those type sites. The same is true for winter habitat and brooding habitat.

Population Recovery

Sage grouse have a relatively low reproductive rate and the ability to recover from population reductions is low (BLM 1999c). Sage grouse have low fecundity, low adult survivorship, and very low productivity. Their recovery time when threats are removed is slow, as is that of their habitat. As Connelly, et al. (2000e, p. 981) put it, sage grouse "populations that have thus far survived extensive habitat loss may still face extinction because of a time lag between habitat loss and ultimate population collapse."

Time lags may be common for birds in shrub-steppe habitat, and they have been noted in a number of avian population studies in sagebrush shrub-steppe (Rotenberry and Wiens 1978; Wiens and Rotenberry 1985; Wiens 1985a; Wiens, et al. 1986; Wiens 1989b, II, p. 114 (summarizing)). Once degraded, sage grouse habitat may not recover for many years, even if cattle grazing in halted (Coggins 1998). Besides these time lags in habitat responses *per se*, time lags also occur in species responses after habitat is fragmented (Cowlishaw 1999, Rosenberg and Raphael 1986). The rebounds in sage grouse populations in the 1930s in Colorado and some other states are not comparable to potential rebounds in the future – habitat is more degraded, populations are more fragmented, and virtually all threats are much more severe and imminent than previously. Moreover, sage grouse now face range-wide threats from climate change which were not a significant factor half a century ago.

Time to extinction is not the metric of interest in an endangerment analysis; instead, the time until the species is unrecoverable is the most important concern. If the species declines to a point at which it cannot be recovered, it must inevitably become extinct at some time. For species which have difficulty in increasing their numbers from small populations – such as sage grouse – the differences between these two time periods is significant. Once the species, subspecies, or distinct population segment is no longer recoverable, extinction is inevitable. The Service should estimate the time remaining until populations of sage grouse are so small as to be unrecoverable. Dr. Clait Braun, perhaps the most acknowledged expert on sage grouse throughout their range, believes that if spring counts decline below about 50 to 100 birds, then the population will be unrecoverable (Braun 2001h).

The Service has recognized the important effects on extinction risk of demographic stochasticity, environmental stochasticity, natural catastrophes (such as fire and drought), and genetic stochasticity (Shaffer 1981). At the time of publication, Dr. Shaffer was a FWS biologist in the Office of Migratory Bird Management (Shaffer 1981, footnote, p. 131). The effects of

these and other factors on population viability have been addressed in modeling exercises with varying degrees of empirical testing and validation. Boyce (1992) and later Beissinger and Westphal (1998) have summarized various population viability model (PVA) categories and discussed their data requirements. Viability analyses that do not estimate lower confidence intervals, or that fail to consider the effects of rare, but severe episodic events will be "unduly optimistic" in their assessment of population viability (Ludwig 1999). For example, when two known severe population declines were excluded from a data set, the probability of extinction calculated was "quite small;" however, the declines greatly increased extinction probabilities (Ludwig 1999, p. 304). There is always variance around any measurement of population phenomena, and additional variance around any model estimate – consequently, the Service should err on the side of conservation in considering both data and model outputs. Importantly, the Dept. of Interior has noted that population declines have exceeded estimates of the rate of decline in past recovery efforts (Pattee 1995, Fig.).

Small Population Size

Sage grouse are now typically found in small populations, and small population size is itself a threat to such species, even if no trend towards even lower numbers is seen. It has long been known that demographic and genetic stochasticity are important determinants of extinction risk (Shaffer 1981). Both these risk factors increase in small populations. The Service recognizes that stochastic perturbations can "extinguish populations even in an environment that, on average, is favorable for their growth and persistence" (Shaffer 1981, p. 131) and must take this crucial factor into account when evaluating a potential listing. The Service cannot assume that an increase in population size removes extinction risk, unless the populations are sufficiently large that stochastic effects are negligible. As Poethke, et al. (1996) note, virtually all models of population dynamics predict geometrically decreasing persistence time of a population as population size decreases. This is true of traditional birth and death demographic models, as well as Markovian chain approximations and Monte Carlo simulation approaches (Poethke, et al. 1996, p. 83). Simple analytical models are inadequate for assessing population extinction probabilities, and generally underestimate the risk of extinction (Shaffer and Samson 1985). Deterministic models, in general, also underestimate extinction risk (Beddington and May 1977, Caswell 1989). As one example of the rapidity of extinction in ground dwelling birds, the Heath Hen (*Tympanuchus cupido cupido*) was given an island refuge and predators were controlled. Yet, the species became extinct in only 14 years, although over 800 individuals were present in the population (Shaffer 1981, p. 131). The Population Assessments section, below, discusses examples where grouse became extirpated without downward trends in population size.

Small populations are at high risk of extinction for several reasons, including loss of genetic variation through inbreeding or genetic drift, demographic fluctuations (such as variation in births, deaths, or age classes), and environmental fluctuations (such as variations in predation rate, disease or parasitism rates, climate, episodic weather events, competition, food supply and a host of other abiotic or biotic factors). Inbreeding depression, and perhaps other factors, show up preferentially in fitness characters such as fecundity, juvenile mortality, and age at first breeding, because those characters typically display dominance or over-dominance (Frankel and Soule 1981, p. 65). Inbreeding depression can affect all individuals in a population (Hedrick and Kalinowski 2000).

Until the early 1990s, classic population genetics theory had not often been expanded to consider the effects of weak selection, environmental fluctuations, strong population subdivision, different aspects of inbreeding, and cumulative weakly deleterious mutational loads (Loeschcke and Jain 1994a, p. 87-88). As analysis of population viability has expanded to incorporate additional factors, population persistence estimations have decreased. For example, when environmental fluctuations are added, persistence times increase only linearly with population size (Shaffer 1987) or only logarithmically (Wissel, et al. 1995), resulting in increased risk of extinction at even larger population sizes (Poethke, et al. 1996, p. 83-84). Thus, if the Service finds that contemporary viability models do not include all factors affecting demographic variables, or more likely, that not all factors affecting demographic variables are known with precision, it must err on the side of caution to fulfill the legislative mandate in the ESA.

Shaffer (1981, p. 133) reviewed the history and limitations of arbitrary rules of thumb, such as the "50/500 rule." Briefly, the 50/500 rule considered only genetic effects and did not account for the need to preserve long term evolutionary potential. When it first arose over two decades ago (Franklin 1980, Soule 1980), the lower limit of $N_e = 50$ was thought to prevent unacceptable short-term rates of inbreeding, and the N_e of 500 was thought to maintain genetic variability. Neither figure is, or was, intended to incorporate demographic or environmental stochastic factors. Such "magic numbers" as the basic 50/500 rule are suitable for informing lay audiences about the general dangers of small population sizes, even though subject to misunderstanding and misuse (Soule 1987). NMFS recognizes this and has noted criticisms of the 50/500 rule, including the arbitrary choice of 1% inbreeding, the assumption that selection is zero in wild populations, and others (Thompson 1991, p. 6, 25). As Culotta (1995) notes, more recent studies show that substantially higher population sizes are required to prevent extinction.

The best available science requires a minimum N_e of 5,000 for population viability (Lande 1995). This viability requirement for N_e translates to a census population of 10,000 to 20,000 individuals or more (Culotta 1995, Noss 2000). This is particularly true for populations that have been gradually reduced in size over time, such as sage grouse (Lande 1995, p. 786). Another factor which interacts with genetic phenomena is environmental fluctuation – such changes in the environment are likely to have fitness consequences, resulting in a high degree of variance in selection coefficients, which in turn "drastically decreases the mean time to extinction" (Lande 1995, p. 787). Such extinction risks are comparable to those from environmental stochasticity even for merely reasonable levels of variance of selection coefficients (Lande 1995, p. 788). Mutation load of even slightly deleterious mutations "considerably enhances extinction risk for small sexual populations if it acts together with demographic stochasticity" (Gabriel and Burger 1994, p. 69; Gabriel, et al. 1991). Classical models of demographic stochasticity typically underpredict extinction risk (Gabriel and Burger 1992). Moreover, smaller populations face much greater synergistic interactions among risk factors, greatly amplifying overall extinction risk (Gabriel and Burger 1994, p. 70). Population sizes of 10,000 or more may be needed to maintain single-locus traits, such as disease resistance, which has been suggested as an important mating system effect in sage grouse (Lande 1995, p. 789; Boyce 1990). Moreover, synergistic interactions among risk factors must be considered in determining population viability, and such interactions likely require minimum population sizes greater than 10,000 individuals.

The Service has agreed that these population sizes are needed for viability. Mr. Terry Ireland (a FWS employee in Grand Junction, Colo. who is familiar with sage grouse) stated that "10,000 individual birds are necessary to maintain a population for 100 years" (Summary of North Park Working Group Meeting 1999, p. 6). Because 100 years is an easily foreseeable time frame, this determination alone requires listing. Besides the Service, federal land management agencies also recognize the extinction risk of small population size: "Smaller and more isolated disjunct populations are likely more susceptible to local declines or extinctions" (Marcot, et al. 1997; Quigley and Arbelbide 1997a, p. 77).

A population below the minimum size for viability must, *ipso facto*, be legally endangered. All populations smaller than about 10,000 individuals should be considered endangered, unless the best available scientific information can show that such populations are, for some reason or other, not in danger of extinction. For all known populations of sage grouse, the factors discussed here indicate that even much larger census sizes will be endangered.

A number of other factors show that sage grouse are likely to be even more at risk than other vertebrates with similar population sizes. Marginal populations are likely to be less variable than central populations, thus increasing the likelihood of extinction in such peripheral isolates. Peripheral populations may also occupy less favorable habitat, further increasing their risk of extinction (Wilson 1975, p. 113).

Sage grouse populations fluctuate with environmental conditions, and the lower the population level, the greater the risk of extinction (Hays, et al. 1998). Lande (1988a, 1988b) and later Caro and Laurenson (1994) noted that while genetic variation issues are serious and perhaps irreversible problems, environmental and demographic fluctuations are likely to cause the greatest risk of extinction in the near term. Vrijenhoek (1994) showed that genetic correlations can arise in small isolated populations, and that remnant variation is likely to be correlated with fitness, thus affecting population viability. Vrijenhoek's analysis is important both for understanding extinction vortices (*sensu* Gilpin and Soule 1986) and for appreciating the importance of peripheral populations. To ignore such correlations is to fall into the trap of "beanbag genetics" criticized decades ago by Lewontin (1974).

Population trends themselves can constitute risk factors for extinction (Mertz 1971a, 1971b). Populations that have been in declining trends for several generations, as have sage grouse, experience selective environments favoring delayed reproduction, reduced reproductive effort and increased longevity. These are precisely the demographic characteristics that make it more difficult to recover from sharp population declines, and thereby increase extinction risk (Wilson 1975, p. 100; Mertz 1971a, 1971b). The Service recognizes that extinction risk requires a time interval for any meaningful definition, and a minimum viable population size must be sufficiently large to "endure the calamities of various perturbations and do so within its particular biogeographic context" (Shaffer 1981, p. 132). The National Marine Fisheries Service (NMFS) has also noted that the definition of "danger" does not imply a sense of immediacy – the term peril connotes immediacy of hazard (Thompson 1991, p. 2). Thus, the Fish & Wildlife Service must define risk of extinction over some fairly lengthy quantitative time period to avoid an arbitrary or capricious listing action. A definition which requires immediacy, as has been used by FWS in the past, appears to conflict with the Congressional mandate in the statute. Moreover, the Fish & Wildlife Service should defer and coordinate its listing policies with those of its sister

agency responsible for listings, NMFS. The above threat factors, and others, are discussed further under each topical heading below.

Loss of Genetic Variation

Small populations face increased susceptibility to chance environmental and demographic effects, and also typically lose genetic variation due to drift, inbreeding or other population phenomena (Lande 1988a, 1988b; Caro and Laurenson 1994). Loss of genetic variation reduces mean population fitness and decreases the ability of the population to respond to environmental stressors (Westemeier, et al. 1998). Drift, founder effect, inbreeding and other factors causing reduced genetic variation increase as population size decreases and ultimately reduce fitness and survivorship (Allendorf and Leary 1986; Roelke, et al. 1993; Lacy 1987). Rare alleles are lost more rapidly in small populations, as is the proportion of heterozygous genes per individual and in the entire population (Avise 1994, Gyllensten 1985). This effect is known from populations of wild vertebrates (Soule and Mills 1998).

Sage grouse are even more susceptible to inbreeding depression because the lekking system greatly reduces the number of males which breed, radically reducing population size (Young and Minchella 1997, Bradley and Donnelly 1999, p. 25). Westemeier, et al. (1998) report a study on a species related to sage grouse, the greater prairie-chicken (*Tympanuchus cupido*), which also leks. Populations of greater prairie chickens may have become trapped in an "extinction vortex" (*sensu* Gilpin and Soule 1986) where loss of genetic variation interacts synergistically with demographic and environmental stochastic effects to drive populations to extinction. Populations of the greater prairie chicken, like those of sage grouse, exist in a series of isolated relicts with little habitat connections and only sporadic gene flow to restore genetic variation. The breeding population remained smaller than 500 individuals for 35 years. Prairie chicken population size, productivity, genetic heterogeneity, and fitness decreased even though both habitat quality and quantity increased, and predation and nest parasites were controlled (Westemeier, et al. 1998, p. 1697). Thus, both current and planned methodology to enhance sage grouse populations may prove ineffective.

Demographic Stochasticity

In small populations, r fluctuates due to demographic effects, even in a constant environment. Small populations thus suffer erratic swings in size due to demographic stochasticity, and at the same time, such small numbers provide no buffer against declines in numbers resulting in extinction. Because sage grouse exist in small demes (sub-populations) they are particularly susceptible to such effects. Moreover, sage grouse are subject to strong demographic effects of environmental variation on vital rates. This has strong effects on extinction risk. Populations "numbering many thousands may be at risk" in species "subjected to intense environmentally driven variation in life history parameters" (Quinn and Karr 1993, p. 452; Leigh 1981). Sage grouse is just such a species. Extreme variability in population size suggests "considerable risks of extinction in even locally abundant populations" (Quinn and Karr 1993, p. 452). This environmentally driven variation in vital rates "can lead to a substantial short term risk of extinction" even when a population is growing in size (Quinn and Karr 1993, p. 460).

The recovery time of populations subject to demographic stochasticity strongly affects extinction risk. Extinction risk also increases sharply as carrying capacity (K) decreases (MacArthur and Wilson 1967), and is strongly affected by r_m (Lande 1993). This factor is low in sage grouse, further increasing the likelihood of extinction. When the long-run growth rate is negative, extinction risk scales logarithmically with initial population size (Lande 1993, p. 912, 923). This result indicates that sage grouse are faced with extinction throughout their range, as no populations show long-term positive growth rates, even the largest ones.

Effective population size is also affected by the variance in production of progeny among individuals (Lande and Barrowclough 1987). Because of their breeding system, it would be difficult to find a species with greater skewness of reproductive contribution than sage grouse. Thus, all census estimates of population size must be reduced by the operation of demographic effects to adequately assess extinction risk. Demographic stochasticity can be an even greater threat to small populations than is genetic stochasticity (Westemeier, et al. 1998).

Environmental Stochasticity

May (1973b) may have been the first to distinguish between the effects of demographic and environmental stochasticity. Contemporary models of metapopulation dynamics often assume that persistence depends on the balance of extinction and colonization in a static environment (Hanski 1996). Environments are not static, however, particularly the grass and shrub lands that constitute the habitat of sage grouse. Besides extreme climatic variation, these habitats are being reduced in size, degraded in quality and fragmented at rapid rates. Large and unpredictable fluctuations in climatic and other environmental factors are known to occur frequently across the entire range of the species. These are thus anticipated risk factors that must be considered by the Service – no one can claim that these fluctuations are unanticipated natural events. Moreover, biotic ecosystem components exhibit more variability than do abiotic components, and animals exhibit more variability than do plants (Kratz, et al. 1995). Finally, environmental stochasticity can be more important than genetic or demographic stochasticity, especially in populations of moderate or greater size (Lande 1988a). This fact has been recognized by both NMFS (Thompson 1991, p. 4) and FWS (Shaffer 1987).

Environmental stochasticity can be fully examined only if the factors of predictability and amplitude of effect, as well as the periodicity and contingency of environmental variation are considered (Colwell 1974, Stearns 1981). Duration of effect, recovery time, spatial distribution, and frequency are other important metrics for evaluating disturbance effects (Sousa 1984; White and Pickett 1985; Wiens 1989b, II, p. 113). One of the major errors in the conservation planning for spotted owls was that environmental stochasticity not considered (Noon and McKelvey 1996, p. 148); consequently, the population models were overly optimistic and owls remain at risk.

Climatic and weather effects have long been recognized as primary factors affecting terrestrial populations (Allee, et al. 1949, chap. 22; Andrewartha and Birch 1954, part III; Watt 1968, chap. 11.3; Gessaman and Worthen 1982). Climate and its short-term analog, weather, are particularly variable and unpredictable in sagebrush ecosystems (Miller and Eddleman 2000, p. 15). Because it is located in a continental interior, the range of sage grouse is often completely affected by climatic effects such as drought – no spatial refugia exist for the species. Moreover, sage grouse are "particularly susceptible" to the effects of drought (Storch 2000b, p. 63).

The ecosystem type inhabited by sage grouse is subject to more extreme fluctuations than most ecosystem types in North America, and is less temporally predictable (Noy-Meir 1973; Wiens 1974a). Shrub-steppe areas have "considerable climatic variability" on both short-term and long-term bases (Rotenberry and Wiens 1980b, p. 2), and have a "highly unpredictable climate" (Wiens 1976, p. 89). Miller and Eddleman (2000) note that the range of sage grouse is characterized by a "high degree of landscape variability and yearly weather fluctuations." It is thus highly likely that sage grouse populations will be subjected to periodic reductions and consequent genetic bottlenecks, further increasing the risk of extinction to the birds.

Moreover, environmental variation affects the ability of humans to manage ecosystem effects. Short-term variations in local or regional precipitation – upon which management planning often is based – are greater than the predicted change in the mean value of precipitation for North America (Shuttleworth, 1996).

Drought is perhaps the major climatic variable affecting sage grouse productivity and viability (Klebenow and Gray 1968; Peterson 1970b; Drut, et al. 1994a, 1994b; Gregg, et al. 1994). Drought is common within the range of the sage grouse, and precipitation deficits of 85% or less of the mean occur 20% to 30% of the time (Miller and Eddleman 2000, p. 15). These climatic regimes may last from 2 to 21 years and can affect plant distribution as well as their more immediate direct effects on sage grouse (Miller, et al. 1993). Drought events appear to be associated with extra-tropical oceanic circulation patterns (Miller, et al. 1993) and are exacerbated by global warming. Declines in sage grouse populations during the 1930s are strongly related to the drought in the continental interior at that time (Patterson 1952c). Populations recovered in most states in the 1950s (see Population Assessments sections) immediately after the period of abundant rainfall in the west during the World War II years (Malone and Etulain 1989, p. 111-112). Drought from the mid-1980s to the mid-1990s has also been suggested as a cause of sage grouse declines in Oregon and Idaho (Fischer 1994; Hanf, et al. 1994; Connelly and Braun 1997). In Oregon's Blue Mountains province, drought cycles peaked in the late 1980s and troughs (wet years) occurred in 1977 and the early to mid 1990s (Brooks 1996). In NE Washington state, the mid to late 1980s were also drought years, with wet years occurring in the late 1970s and early to mid 1990s (Brooks 1996, p. 52).

Drought strongly affects the food supply of both gravid females and maturing young sage grouse, and affects cover providing concealment and radiative and wind buffering (Autenrieth 1981; Hanf, et al. 1994; Fischer, et al. 1996b). Drought effects are particularly severe in areas that are overgrazed, and will "exacerbate the adverse effects of heavy, excessive livestock grazing on vegetation and soils" (Nevada State Office, BLM 2000a, p. 6). BLM acknowledges that excessive grazing has been the case in "many areas" (Nevada State Office, BLM 2000a, p. 6). Periods of low temperature and rain, snow or sleet can also cause nest failures (Patterson 1952c). Population viability models have been previously constructed for species affected by episodic droughts (Armbruster and Lande 1993). Environmental stochasticity can be an even greater threat to small populations than is genetic stochasticity (Westemeier, et al. 1998).

Sage grouse are highly susceptible to variation in precipitation. Rich (1985a) found that about 65% of the variation in juvenile/adult ratios was explained by the amount of precipitation in July and August. Moreover, 8 of 9 monthly weather variables that were significantly correlated with lek counts in Idaho were precipitation measures (Rich 1985a). At higher elevations, temperature may be more important (Rich 1985a, p. 12). Drought and grazing

pressure interact to exacerbate negative effects on sage grouse productivity (Blake 1970). During low precipitation years (less than 15 cm), meadows are critical habitats for sage grouse; unfortunately, they are heavily used by grazing cattle (Oakleaf 1971; Klebenow 1982, 1985; Evans 1986).

"[E]nvironmental stochasticity is a significant threat to Washington's sage grouse" populations (Bradley and Donnelly 1999, p. 28). Because the same effects are equally large or larger in other small populations of sage grouse, environmental stochasticity threatens them also. Many sage grouse populations are at high risk from environmental stochasticity, including weather related factors such as a drought year, a hard and snowy winter, or insufficient spring precipitation. Such events may occur in the next few months, i.e. this winter, spring, or summer, and could affect the entire range of the sage grouse. If these weather events were sufficiently severe, they might cause complete extinction of sage grouse. Even if a lesser severity or magnitude were to occur, a significant proportion of the subspecies would be extirpated. These threats are ongoing in nature and interact with other threats.

Effective Population Sizes

Effective population size (N_e) is a term used to incorporate various environmental, demographic, and genetic effects on population dynamics. N_e has been calculated in various ways, and can incorporate the effects of drift, inbreeding, and loss of alleles at segregating loci (Burgman, et al. 1993, p. 238). The population dynamics of small populations cannot be accurately estimated without consideration of effective population size. This is not a new result; instead, it dates from at least the time of Sewell Wright in the 1940s.

Various estimates of the ratio of N_e to N indicate that effective population sizes will be only 25% to 33% the size of the census population (Soule 1980, Wilcox 1986). Salwasser and Marcot (1986) suggested 50%, but they used unrealistically low minimum viable population sizes of 100 and 1,000. For vertebrates, minimum viable populations should be approximately 5,500 or more (Thomas 1990). NMFS independently derived similar a size of 5,000 (Thompson 1991; p. 8, Appendix B). The Service has used unrealistically low recovery goals for other species, for example the Southern Sea Otter, for which it used a "genetically effective population size of 500" (FWS Southern Sea Otter Recovery Team 2000, p. 25), which led to census population sizes of more than 2,650 for recovery, of 1,850 to 2,650 for the threatened category, and of 1,850 or less for the endangered category (id., p. ix). The Service did not adequately include environmental stochasticity and other effects in its draft determination, however. Schroeder (1998b) applied the N_e concept to sage grouse but only incorporated a subset of the effects. Thus, N_e will be lower than those calculated using the formula given by Schroeder (1998b). However, if used cautiously and conservatively, Schroeder's formulation is a useful metric until population viability models are established for the species. The Service must make its listing determination on the basis of the best available science regarding minimum viable population sizes, however. That science indicates that relatively large census populations are required.

One important effect on N_e in sage grouse is the fact that very few males mate with a large number of females, thus reducing genetic variation. A lager number of studies illustrate this phenomenon: in Wyoming, 2 males obtained 74% of 174 observed copulations (Scott 1942) and 86% of 42 copulations (Wiley 1973b); in Saskatchewan and Montana, 54% of 103

copulations (Lumsden 1968); and 66% of 533 copulations in Montana (Hartzler and Jenni 1988). Gibson, et al. (1991) noted that females are nearly unanimous in mate choice, and Hartzler and Jenni (1988) found a single male that mated 169 times in a single season. Moreover, yearling males are unlikely to mate and occupy disfavored areas on the periphery of the lek (Dunn and Braun 1986b).

An estimate of the effective population size can be made by using simplistic textbook equations (e.g. Meffe and Carroll 1997, p. 173) for N_e based on the monopolization of breedings by a few males. For a liberal estimate of N_e, assume that all birds are in a single population, and that the census population size is 276. There are 92 males and 184 females. Make the further liberal assumption that all of the females breed successfully. If two males garner all matings at a lek, as is often the case in sage grouse, then 8 males have mated with the 184 females. The effective population size for sex ratio effects is given by:

$N_e = \frac{4 * N_m * N_f}{[N_m + N_f]} = \frac{4 * 8 * 184}{[8 + 184]} = 30$, where N_m = the number of males breeding in the population, and N_f = the number of females breeding in the population, and fractional results are truncated. This simple analysis using optimistic, not conservative assumptions, shows that few sage grouse populations are secure – even in the short term. N_f will be further reduced by variation in family size among females, and that effect can be calculated as:

$N_e = \frac{4 * N_c}{\sigma^2 + 2}$, where N_c = size of the census population , and σ^2 = the variance in family size. This formulation does not include the effects of environmental stochasticity, so much larger census populations will be required to produce viable populations. Other factors will also increase the census population size required. N_e also will vary with the spatial dispersion of individuals across a landscape (Hartl and Clark, p. 90), an effect that might be particularly large for sage grouse. Because there are a large number of different factors that affect population dynamics, there are a plethora of ways to calculate N_e – at least as many as the number of mechanisms affecting genetic drift (Boyce 1992, p. 486). Effects of overlapping generations, dispersal and spatial dispersion have been considered by Reed, et al. (1986); Chepko-Sade, et al. (1987); and Harris and Allendorf (1989). Generally, the effects of overlapping generations can cause severe underestimation of the size of a census population required to maintain N_e at a given size and the method of Reed, et al. (1986) will usually underestimate census population sizes (Koenig 1988, p. 232). As with other species having overlapping generations, juvenile and adult sage grouse are not equally likely to breed. In fact, it is rare for juvenile male sage grouse to breed at all. N_e has also been calculated for extinction-repopulation events in a metapopulation (Gilpin and Hanski 1991). Incorporation of additional factors in more complete models will further reduce effective population size and hence persistence time.

Allee Effects and Social Disruption

The term Allee effect refers to the negative effects on population processes of low population size or density (Allee 1938, 1951; Drickamer and Vessey 1992), sometimes also termed "undercrowding." Sage grouse are likely to show significant Allee effects because of the lekking habit – if the number of males declines sufficiently, the joint signaling function of having many males undergoing simultaneous sexual display and the advantage to females of gathering information regarding multiple males will both decline. Thus, as lek size decreases, the

advantage of lekking collapses, at some threshold value. This is borne out by the numerous reports of lek abandonment below a threshold size. Other types of Allee effects are also likely to occur in sage grouse, including the difficulties of finding a mate (Dennis 1989), the ability to evaluate numerous potential mates for suitability, difficulty in detecting, evading or fending off predators or competitors (Boyce 1992, p. 493). Allee effects appear ubiquitous and occur across a wide range of taxa: for example, Allee noted that groups of fish survived toxic conditions better than single fish, as did groups of flatworms. Moreover, all the benefits of group size for predator protection and other ecological interactions (summarized in Wilson 1975) are lost when group sizes decrease. All available evidence points to substantial decreases in sage grouse group sizes. Soule (1983) notes that social disruption is likely to cause extinction long before genetic effects such as drift or inbreeding and long before demographic stochasticity. Even species with "high reproductive potential are vulnerable" and that a minimum viable population size may be two orders of magnitude larger when social disruption is involved (Soule 1983, p. 118). Soule specifically mentions two other species of grouse – the Heath hen and Attwater's Prairie Chicken – as examples of extinction thresholds being crossed despite high reproductive potential (Soule 1983, p. 118).

Because of Allee effects, decreases in population size are unlikely to be linear; instead, as population size decreases to some threshold value, rapid declines and extirpation are likely. Such declines may be so rapid as to be undetectable before they actually occur, or if detected, extirpation may not be preventable by that point. Certain aspects of the environment combine with Allee effects to greatly increase the likelihood of extinction for sage grouse. First, Dennis (1989) has shown that environmental stochasticity amplifies Allee effects. As explained elsewhere in this review, sage grouse populations fluctuate greatly and sage grouse habitat are subject to great amplitudes of environmental stochasticity as well as unpredictability of these fluctuations. Second, "harvesting also amplifies those [Allee] effects" (Dennis 1989, p. 481). Thus, hunting of sage grouse can greatly increase extinction risk, and this risk will not be accounted for in conventional models of population harvest. Petitioners request that the Service consider this and all non-linear effects of population declines in evaluating the status of sage grouse species. This is particularly important because non-linear, or threshold effects may cause populations that "appear safe for many years" to "decline suddenly" (Meffe and Carroll 1997, p. 218). Pulliam (1992) already modeled a situation similar to that for sage grouse –an example in which the population abruptly declines as the proportion of agricultural areas in the landscape increases. Such declines are difficult to predict "because the problem may well go undetected until a critical threshold is reached" and causes "catastrophic population collapse" which has been documented repeatedly (Meffe and Carroll 1997, p. 219). One of the major errors in the conservation planning for spotted owls was that Allee effects were not considered (Noon and McKelvey 1996, p. 148); consequently, the population models were overly optimistic and owls remain at risk.

Cultural Inheritance

Modern behavioral ecology has documented numerous instances of cultural inheritance in non-human species (sometimes termed "memes"). Young sage grouse learn from older sage grouse (SMBCP 1998, p. 22), and thus important survival behaviors can be lost from the population if cultural transmission is interrupted. This effect operates most strongly in small

populations, just as alleles are lost most frequently in small populations. Social disruption, and the removal of older more experienced individuals from a population, as in trophy hunting, can also be expected to remove learned behaviors from the population (Wilson 1975, p. 152, 168-172). Connelly, et al. (1988) suggested that seasonal movements may be traditional, hence culturally inherited. For example, roads often eliminate traditional movements from sage grouse populations because older, more experienced sage grouse are eliminated from the population by road deaths (SMBCP 1998, p. 22).

Thus, deaths of relatively old, post-reproductive grouse may have important population effects (contra Braun 1995e, p. 1). However, sage grouse only rarely live to be post-reproductive, so this potential cultural effect may be of merely theoretical importance.

Population Cycling

Sage grouse populations have been suspected to cycle for some time (Patterson 1952c). Rich (1985a) used power spectrum analysis to analyze 39 leks in Idaho, Utah, and Nevada, and found significant periodicity ranging from 8 to 10 years. Cycling populations have greater extinction risk for two reasons. First, they periodically experience low population sizes, with all the concomitant risk factors of small populations. Thus, it is not the periodic population maxima that are of greatest importance for population viability, it is the periodic population minima. Second, cycling populations may be composed of behavioral and genetic types of individuals who are adapted to high population numbers, but are then exposed to low population sizes that they are ill equipped to deal with. Similar arguments apply to species with longer lived individuals whose lifespan is greater than the periodicity of the cycles, except that such individuals are not adapted to large population sizes. Instead, they would be either developmentally canalized or physiologically acclimatized to high population size, and then exposed to very low population sizes during their lifetimes.

Climatic cycles are common in the sagebrush region inhabited by sage grouse and typically last from 2 to 21 years (Miller, et al. 1993, p. 108). It is tempting to hypothesize that sage grouse population cycles are driven by climatic cycles. Apparently, no studies have analyzed this linkage, and the entire realm of population cycling has generated a ponderous literature across many different species, ecosystems, and continents without resolving the issue. In the Great Basin, periods of increased precipitation are better known and "are probably associated with El Nino" events and other extra-tropical alterations in oceanic circulation (Miller, et al. 1993). Cycles in various species of grouse are not synchronized with those of lagomorphs or rodents, and tend to lead the mammalian population declines, suggesting that predators do not drive grouse cycles (Hoffmann 1958).

Hamerstrom and Hamerstrom (1961) noted that sage grouse were subject to dramatic changes in abundance. Importantly, it is not known if sage grouse are even adapted to fluctuations in population size. No studies were undertaken of the birds before cattle and sheep grazing degraded the shrub-steppe. It is known that population fluctuations are greater in marginal habitat (Rich 1985a, Linden and Rajala 1981, Jenkins, et al. 1967; Hilden 1965; Rowan 1948). Furthermore, even if the birds are adapted to cyclicity, it is not clear that they are adapted to the degree of cyclicity that they now face, because a given variation in a climatic factor, such as precipitation, may have profoundly greater effects in degraded and fragmented habitat than it would in intact habitat. The likelihood that sage grouse are cyclic should not be used to excuse

or hide mismanagement. As Connelly noted, there are "not any stable habitats" remaining that can be used to determine if sage grouse are truly cyclic or not, and "labeling a population as cyclic is dangerous because it is often used to excuse mismanagement" (Heath, et al. 1996a, p. 3, citing Connelly during discussion). Nonetheless, population numbers are subject to "dramatic fluctuations" (Schroeder 2001a), complicating management and recovery (Rich 1985a), and making extinction more likely than in more stable populations.

Reintroductions

Reintroductions of species are difficult and expensive. Once community structure is altered, introduction of a species – even one previously present in the community – can be difficult (Diamond 1975b).

Johnsgard (1983, p. 99) noted that there were few instances of successful propagation of grouse, thus complicating the recovery of populations that fall to very low levels and the introduction of sage grouse to their historic range (Batterson and Morse 1948; Pyrah 1963). Patterson (1952c, p. 300) noted that reintroductions and transplanting of sage grouse in Wyoming apparently had only token results, even when "extensive releases' were conducted. A more recent review also concluded that reintroductions of sage grouse were rarely successful (Reese and Connelly 1997). Reintroduction was tried in Montana with 242 sage grouse at 8 sites, but was unsuccessful (Martin and Pyrah 1971, p. 135). Reintroductions from captive breeding programs may have lower fitness than natural populations, and such programs may allow deleterious genes or gene combinations to increase as captives are provided with ad lib food, medical care, and a predator free environment (Caughley 1994). Captives are also likely to lose essential behaviors if there is any component that is transmitted culturally. Moreover, it has never been demonstrated that an extinction can be prevented by any reintroduction (Fyfe 1978, Berger 1978). Reintroductions also run the risk of introducing disease if a small natural population already exists.

Because reintroductions are so difficult, it is imperative that existing populations of sage grouse be conserved wherever found. It may not be possible to reintroduce sage grouse where they have been extirpated; thus, peripheral isolates are of great importance to recovery of the species.

Importance of Peripheral Populations

Contemporary understanding of evolution and population biology emphasizes the importance of populations at the extremities of a species range. It is in these peripheral populations that the evolutionary potential of a species is greatest (Gadgil and Bossert 1970, Levin 1970, Gadgil 1971). Peripheral populations often differ genetically from more centrally located populations, thus adding genetic diversity to the species and providing genetic backgrounds where natural selection can more easily increase the gene frequency of novel alleles or combinations. "Such populations are often of evolutionary significance" (Scott, et al. 1993, p. 35), and "preserv[e] unique genetic material" which is "restricted to peripheral populations of native species" (Scott, et al. 1993, p. 36; Quinn and Karr 1993). Peripheral populations may be disproportionately important for conserving genetic diversity (Squires, et al. 1998).

Peripheral populations are also often located at the ecological limits of the species, thus exposing these novel genetic combinations to environmental circumstances that may later

become prevalent in central populations, such as global warming effects. Such testing of the periphery can act to stabilize the entire species in the face of environmental change.

Rapid evolution is likely when a peripheral population is isolated from gene flow, allowing a local deme to evolve to a local ecological optimum (Garcia-Ramos and Kirkpatrick 1997). Such evolution can be the first step to speciation, independent of genetic drift ("genetic revolutions," *sensu* Mayr 1963, 1982) or founder event mechanisms (Carson and Templeton 1984). Quantitative traits have very high mutation rates (1 per 1,000) as opposed to the mutation rates typical of other loci, and are thought to be more closely related to fitness than are other traits (Lande and Barrowclough 1987; Nei 1987).

The importance of peripheral populations is likely to increase with climatic change (Hunter 1991; Quinn and Karr 1992; Scott, et al. 1993). Peripheral isolates are also of great importance to recovery of species where reintroduction is difficult, such as sage grouse.

Geographical Distribution

Historic Range

The historic range is based primarily upon accounts from the early 1900s and late 1800s. The range of sage grouse before Euro-American settlement of the west is unknown but likely exceeded that reported in the 1930s through the 1950s, because of the severe destruction of grass and shrublands caused by the overgrazing of livestock from the late 1800s to the early 1900s. Attempts to reconstruct the extent of the range prior to Euro-American settlement are difficult because this widespread habitat destruction occurred before scientific study took place, except for a few surveys. Thus, the pre-settlement range was likely larger than any estimates that have been presented in the literature. The historic range extended at least across all states of the Intermountain West in sagebrush shrub-steppe habitat, including eastern Oregon, eastern Washington, Saskatchewan, Alberta, southern British Columbia, and the panhandle of Oklahoma and the area of Kansas immediately north of Oklahoma (Schroeder 2000a). Their historic status in Kansas and Arizona is unclear (GBCP 1997, p. 5). In Arizona, sage grouse were last cited in the vicinity of the Grand Canyon in 1937 (Smith 1999). The range of sage grouse thus extended across at least 15 (probably 16) states and 3 Canadian provinces (AOU 1983, Aldrich 1963, Johnsgard 1973, Braun 1995, Reese and Connelly 1997). The Service stated that Greater (Northern) sage grouse formerly inhabited 12 states and 3 Canadian provinces (FWS 2001d, 66 Fed. Reg. 22984, 22985). Of the 15 or 16 states occupied by any sage grouse species, it is likely that the small portions of Oklahoma, Kansas, and possibly Texas occupied by sage grouse in historic times were occupied by Gunnison sage grouse.

Habitat conversion, invasion of various tree species, and other effects have reduced the range in historic times. For example, "sage grouse remains were unearthed" in the wooded Carson Desert Wetlands on the Stillwater National Wildlife Refuge "suggesting that the vegetation composition in the surrounding lower slopes of the mountain ranges was different historically" (US FWS, Stillwater NWR 2000, p. 2-34).

Researchers have compiled a number of maps presented giving the historic range of sage grouse, including Aldrich (1946); Patterson (1952c); Edminster (1954); Johnsgard (1973, 1983); Drut (1994); and more recently, Schroeder (2000a). Johnsgard largely followed Patterson (1952c) in preparing his range map (Johnsgard 1973, p. 159, Fig. 22). Apparently, no recent

comprehensive effort has yet been made to generate a dot distribution map depicting all collected museum specimens to evaluate the various range mapping efforts over the years, or to assess the combined specimens located in various museum collections. However, early on, the Service did present a dot distribution map of collected specimens along with the historic range of the bird (Aldrich and Duvall 1955, p. 2, and map, p. 12). Both Clait Braun (Braun 2001d) and Mike Schroeder (Schroeder, personal communication, Sept. 2000) have made inquiries at the Smithsonian and at most other major museums, as well as placing advertisements in ornithological journals. These data were included in the historic range map compiled by Schroeder (2000a), which is largely based on Aldrich (1946, 1963) and Aldrich and Duvall (1955), according to Schroeder (personal communication). The data and field notes from the US Army Railroad and other surveys were not investigated for the Schroeder (2000a) map according to Schroeder (personal communication). Mapping staff at the Washington DFW used the above data, Kuchler's vegetation map (1964a) and standard USGS topographic maps to produce a "best estimate" of the historic range before Euro-American settlement (Schroeder, personal communication). The California portions of the map were digitized by California DFW (Schroeder, personal communication).

The map of the current range (Schroeder 2000a) was prepared as an initial draft which was then reviewed by sage grouse experts in each state Although the map compiled by Schroeder (2000a) is still considered a draft, it is "relatively close to completion" (Schroeder 2000c) and represents the best estimates of the historic range and of the range in 2000. Schroeder (personal communication) considers the map of the current range to be most accurate in the states of Washington, Utah, Colorado, and California; and least accurate in the states of Nevada, Wyoming, and Montana; with intermediate levels of accuracy in Idaho and Oregon. In Nevada, many areas within the range have very sparse populations and the same is true in Wyoming (Schroeder, personal communication). In Montana, some areas show as within the sage grouse range, but surveys across the border in Alberta have no birds (Schroeder, personal communication). This suggests that the range shown in Montana is overly optimistic.

However, the data on which the map was based were a few years old, and because threats are ongoing, somewhat less of the range is occupied currently than is shown in Schroeder (2000a). Most of the historic range has been eliminated in the intervening decades. Scott, et al. (1993, p. 20) gives a general discussion of such issues, and Connelly and Braun (1997) do so for sage grouse.

As range maps are typically presented, they include large areas that are not sage grouse habitat. Such gaps are common in small scale range mapping or where habitat types are not validated with a dense spatial pattern of on the ground surveys (Scott, et al. 1993, p. 20). The presence of such gaps is easily seen by comparing such range maps with maps of the extent of sagebrush habitat – for example, the map given by Franklin and Dryness (1973, p. 45, Fig. 27) or Paige and Ritter (1999, p. 3). It is unclear whether Patterson, and those who have followed him, included such considerations in their calculations of the extent of sage grouse habitats. The true pre-settlement range of the sage grouse may be even greater than has ever been estimated because the bird is known to have declined before any mapping of the range was undertaken. However, Schroeder disagrees (Schroeder 2001d), noting that there may have been local range extensions if human crops made food available in areas that were previously food limited, and

Spanish settlement may have reduced the range in the southwest prior to 1800 (Schroeder 2001d).

Early Accounts

Before Euro-American occupation of the west, sage grouse were extremely abundant, and huge flocks of the birds were often described (Drut 1994). Flocks consisting of thousands of birds were "common" (Edminster 1954, p. 115). Historic reports describe sage grouse as abundant throughout their range (Coues 1893, Huntington 1897, Burnett 1905; Grinnell, et al. 1918; Rasmussen and Griner 1938; Patterson 1952c). Accounts variously describe gigantic clouds of the birds so large they blocked out the sun, birds so thick that one could get dinner by hitting them with a stick, and birds so abundant that they acted as a control agent for grasshopper outbreaks. Sage grouse were so abundant that they appeared in "flocks that blackened the sky" (Patterson 1952c, p. 19), and were comparable to "the original passenger pigeon flocks" (Patterson 1950a, p. 384). Travelers along the Oregon Trail often feasted on sage grouse, and the birds often "rose up before the wagon trains in clouds of hundreds and thousands" (Cade 1999). Long-time Montana residents also reported that "sage grouse were so plentiful that when they got up they darkened the sky" (Eustace 1995, p. 24). In Wyoming, sage grouse were once so numerous that people were able to gather eggs for table use (McDowell 1956 p. 6). Bendire (1892) quoted field notes from George Bird Grinnell that the sheer numbers of sage grouse reminded him of the "oldtime flights of passenger pigeons" he had seen as a boy. After this reminisce, Grinnell continued, describing the sage grouse as so numerous that they transformed the entire valley into a "moving mass of gray" (Bent 1932, p. 309; Patterson 1952c). In many Western towns, butcher shops offered "prairie chicken" for sale along with other game, and Audubon often frequented these shops for specimens to draw (Brown 1994, p. 170).

Today, these accounts seem almost mythological – the result of over a century of habitat degradation and destruction. The oldtime flights of sage grouse have joined the oldtime flights of passenger pigeons as historical relicts of the once great North American wildlife fauna, and the sage grouse is following the passenger pigeon towards extinction. No one today has a living memory of the biomass and ecological dominance of sage grouse in the West, just as no one has a living memory of the tremendous numbers of buffalo on the plains or the rivers crowded with salmon. What is more, no one today has a living memory of how pristine sage grouse habitat appeared. Sage grouse were an important food source for Native Americans and were commonly eaten by early settlers, until near the end of the 1800s when "encroachment of the white man on the range" created "serious decline" which "became critical soon after 1900" (Edminster 1954, p. 115).

Lewis and Clark reported sage grouse at the head of the Missouri River, on the plains of the Columbia, and at the mouth of the Snake River (Coues 1893, p. 868-869). They repeatedly describe the birds as present in great abundance. Their first report on Sept. 17, 1804, noted that "grouse, larks, and the prairie bird are common in those plains." On Sept. 30, 1804 Captain Clark related descriptions of the "white-booted turkey [prairie cock]" along the Cheyenne River. On Oct. 4, 1804, they "saw great numbers of prairie hens" along braided river channels. On April 14, 1805 Captain Lewis "met with great numbers of grouse or prairie hens" which were mating. Coues notes that Lewis and Clark had "repeatedly" sighted sage grouse by the time they reached the intersection of the Yakima River with the Columbia River on Oct. 17, 1805 (Coues

1893, vol. 2, p. 642, n. 17). Along the plains of the Columbia River, they found sage grouse "in great abundance" all the way from the "entrance of the southeast fork to Clark's River" (Coues 1893, p. 868). It is interesting that Lewis and Clark often saw the birds along major river courses: this suggests either modern-day ecosystem alteration, such as channelization by dams, or changes in the habitat affinities of the birds post-settlement, as has been noted for big horn sheep. In the winter of 1827, naturalist David Douglas reported large flocks of sage grouse along the Columbia River between its confluences with the Spokane and Walla Walla rivers (Yocom 1956). There was probably little overlap of sage grouse with grazers such as bison (*Bison bison*), popularly called buffalo, as most sagebrush ecosystems were not grazed in prehistoric times (Mack and Thompson 1982, Daubenmire 1988).

Accounts of Early Trappers

Penetration of the interior West by whites continued even before the return of Lewis and Clark. Trappers and adventurers ("mountain men") traveled widely throughout the West in the early and mid-1800s. One account was that of James Ohio Pattie who recorded his accounts of travels throughout the West, from the Gila to the Yellowstone and upper Missouri (Goetzmann 1959; Pattie 1907). The primary interest of the trappers was beaver pelts and most did not record their observations. Osborne Russell noted in his journal that he knew of only one other trapper who recorded a regular journal, and Russell considered Pattie's journal full of significant errors (Russell 1955, p. 127). Jedediah Smith drew maps and kept records of his travels but the records did not survive (Utley 1997, p. 39, 100). The account by Warren Ferris of his days trapping in the Clark's Fork country was published in the Western Literary Messenger and republished by Paul Phillips in 1940 (Utley 1997, 155, 348). Some success at reconstruction of ecological history has been obtained from compilations of early accounts (Botkin 1996), so I include a brief synopsis of travels into and near the historic sage grouse range for the motivated ecological historian.

John Colter traveled through the Bighorn basin and the upper reaches of the Wind River country in 1807-08, but this took place during winter (Utley 1997). That spring, one excursion from that expedition traveled along the Bighorn and Little Bighorn Rivers and to the upper reaches of Rosebud Creek and the Tongue River (Utley 1997, p. 16). Elements of Astor's expedition, including Wilson Price Hunt, Donald McKenzie and Manual Lisa, journeyed up the Missouri River in 1811, crossed the Big Horn and Wind River mountains, reached the Green River near Union Pass and followed Henry's Fork and then the Snake River down to the Columbia near Walla Walla. On the return journey in 1812, Robert Stuart's party followed the Snake River south to the Bear River in Utah, then traveled north to the Henry Branch of the Snake River, and then over to the Green River, crossing the Continental Divide by skirting the southern edge of the Wind River mountain range, near South Pass. Stuart then followed the Sweetwater, Platte and Missouri Rivers to St. Louis, a route that later developed into the main immigrant trail. In 1819, McKenzie went down the Snake River valley and Bear River to Bear Lake, the most southerly penetration of the Rockies by Euro-Americans at the time (Goetzmann 1959, p. 31). In 1825, Peter Skene Ogden traveled down the Bear River and reached the Great Salt Lake, which had been visited previously in 1824 or 1825 by Jim Bridger, and perhaps by Ettienne Prevost in 1825 (Goetzmann 1959, p. 32). In 1829-30, Ogden ranged south along the western edge of the Great Basin all the way to the Gulf of California (Utley 1997, p. 120).

Several journeys entered the area of Kansas, and the Texas and Oklahoma panhandles where sage grouse formerly persisted. In 1806 and 1807 the Zebulon Pike expedition crossed a portion of this area, and also reached eastern Colorado, probing the Arkansas and Rio Grande rivers (Goetzmann 1959, p. 35, map; Coues 1895). In 1819, Major Stephen H. Long traveled through this area as well as parts of Nebraska and eastern Colorado (Goetzmann 1959, p. 35, map). The Long expedition included several scientists, topographers, and other specialists including the botanist, Dr. William Baldwin, the naturalist Titian Peale, and the zoologist Dr. Thomas Say (Goetzmann 1959, p. 40; Thwaites 1907). This may have been the first penetration by trained scientists into the range of the sage grouse; moreover, the inclusion of topographers suggests that the locations of sightings may have been recorded with a fair degree of accuracy.

Jedediah Smith's account of his first trip across the Great Basin, which he described in a letter to Gen. William Clark, was published in a newspaper (Goetzmann 1959, p. 24; Brooks 1977). In 1826, Smith journeyed from Cache Valley, Utah to the Great Salt Lake and Utah Valley, then striking southwestward along the Sevier River, he crossed the Colorado River and then the Mojave Desert to Spanish California (Goetzmann 1959, p. 49). From there, Smith crossed the Sierras and the central Nevada deserts to the Great Salt Lake. In 1829, Smith traveled up the Columbia River through the Okanagon Valley to Fort Colville and through the Bitterroot Valley across Lemhi Pass to Pierre's Hole (on the West Side of the Teton Range) then to Jackson Hole (Goetzmann 1959, p. 47, map, and p. 50). Smith is also credited as the first American to discover South Pass. Smith was literate and intelligent, and described his journeys in a letter William Clark, reprinted in *Nouvelles Annales des Voyages* in 1828, and his journeys were recorded on maps compiled shortly after his death (Goetzmann 1959, p. 50; Morgan and Wheat 1954, pages 18-19).

Joseph Walker, acting under the aegis B. L. E. Bonneville, traveled across northern Nevada along the Humboldt River to the Carson Sinks, and then south to Mono Lake and across the Sierras by two different routes in 1833 and 1834 (Goetzmann 1959, p. 47, map). Unfortunately, Bonneville's reports were lost by the US Post Office at Council Bluffs, Iowa (Utley 1997, p. 129).

US Army Corps of Topographical Engineers

From about 1840 to 1861, dozens of official expeditions containing scientists were mounted into the West by the US Army Corps of Topographical Engineers. Most entered the range of the sage grouse. These expeditions were analyzed by Goetzmann for his dissertation, which was later published (Goetzmann 1959). Other general studies of the Corps and its expeditions also exist (Burr 1939) as do analyses of the ornithological and botanical collections made. Congress published approximately 60 works dealing with exploration of the West between 1840 and 1860 (Goetzmann 1986, p. 178). The Topographical Corps expeditions are of particular interest in reconstructing the ecology of the West before Euro-American settlement because they carried surveying equipment and trained specialists allowing a fair degree of accuracy in both the identification of specimens and in the location of those specimens. The efforts of the Topographical Corps constituted the largest single scientific expert study since Napoleon took a group of experts into Egypt (Goetzmann 1959, p. 305). Altogether, 106 scientifically trained experts took part in the surveys either as field collectors or museum classifiers (Goetzmann 1959, p. 307). They were assisted by a small army of mapping and other specialists and part-time soldier-naturalists. Scientific results from the surveys were published in

at least 23 articles of the leading journals of the day, and 17 volumes of official reports were published (Goetzmann 1959, p. 311). Secretary of War Jefferson Davis issued two editions of the official compilation, the Pacific Railroad Reports. The first edition consisted of 3 octavo volumes with an additional folio of maps (Davis 1855; Goetzmann 1959, p. 311). The second edition of the Pacific Railroad Reports was issued in 13 different quarto volumes (Goetzmann 1959, p. 312-313). Information on birds was contained in a monograph in the three volumes devoted to zoology and supervised by Spencer F. Baird at the Smithsonian Institution who worked with John Cassin and George N. Lawrence on the monograph (Goetzmann 1959, p. 328-329). This monograph contained notice of all North American bird collections known at the time. This monograph was later privately republished as BIRDS OF NORTH AMERICA. However, there may have been some data reduction from the original field notes or even collections into the monographs and re-publications – the purposes of 19th Century science are not those of modern inquiries. Unfortunately, a fire at the Smithsonian Institution destroyed some records of the Topographical Corps (Goetzmann 1959, p. 466). The remaining records are nonetheless voluminous – more than 88 boxes of documents exist (Goetzmann 1959, p. 461). Besides Goetzmann's (1959) dissertation, several other works summarize the findings of the Topographic Corps. These include Hume's (1942) biography of Army ornithologists, other bibliographical works by Ewan (1950), Ewan and Ewan (1981), Geiser (1937), Meisel (1924), Hasse (1899), Welker (1955), and an apparently unpublished monograph by Thomas Manning, which is referenced in Goetzmann (1959, p. 309, n. 8). Meisel (1924) catalogs all publications from the Topographical Corps expeditions. The various reports discussed here are cited by Goetzmann (1959, p. 467-475 and elsewhere).

John Fremont made two expeditions into the West in 1842, and 1843-1844. In 1842, Fremont traveled up the North Platte River to Fort Laramie (north of the city of Laramie, WY), across Wyoming via the Oregon Trail along the Sweetwater River and South Pass, and along a portion of the Wind River mountain chain (Goetzmann 1959, p. 80-81). A portion of Fremont's party also detoured along the South Fork of the Platte to Fort St. Vrain and then north to Fort Laramie. The entire collection from this expedition were lost in the notorious rubber boat incident on the Sweetwater River. Fremont's official report was published as a Senate Executive document (27th Cong. 3d Sess. Sen. Exec. Doc 243, 1842-1843) and information on the range of sage grouse or sagebrush habitat may be contained in that document. Fremont is known to have collected specimens along the flat country of the Kansas River (Goetzmann 1959, p. 78). These specimens would be important for determining any linkages of sage grouse or sagebrush between the sage grouse populations in Colorado and those extinct from the Oklahoma/Texas panhandle area. Plants were cataloged by Prof. John Torrey (Torrey 1854) although few new species were discovered (Goetzmann 1959, p. 83). In 1841-1842, Wilkes had traveled in the Oregon country as far as Fort Walla Walla and sent the Emmons-Eld party south into California (Goetzmann 1959, p. 85-86; Wilkes 1844).

During 1843-1844, Fremont returned to the West, initially following the regular Oregon Trail route and then turning south to explore along the Kansas River to Big Timbers. Fremont reported that the Crow Indians had named the upper Green River after the sage grouse, and that they were very abundant in the area. The party split at Big Timbers, one group going northward along the Platte River, and the other going straight across the plains, to where they met at St. Vrain's Fort. From there, they explored the Cache la Poudre River, backtracked, and followed

the Sweetwater River to a crossing at South Pass, and then down to the Green River. From there, they traveled to the Muddy Fork of the Ham River and on to the Bear River (Goetzmann 1959, p. 90). The party followed the Bear to the Great Salt Lake and camped near the Weber River. The party journeyed on to Fort Hall, then up the Snake River to Fort Boise and out onto the Columbia Plateau via the Grande Ronde river to the Whitman mission at Walla Walla and then followed the Columbia to the Dalles, lining their surveys with those of Wilkes (Goetzmann 1959, p. 92). Fremont returned to the United States by a circuitous route. He traveled south through Oregon paralleling the Des Chutes (now Deschutes) river to Klamath Lake, then continued southward, paralleling the Sierra Nevada (Goetzmann 1959, p. 95-96). South of Lake Tahoe, Fremont made the arduous winter crossing of the Sierras, in which he again lost all his plan collections when the mule carrying them tumbled off an icy precipice into a river (Goetzmann 1959, p. 98). Fremont descended along the American River and reached Sutter's Fort. From there, Fremont went southward along the Sacramento and San Joaquin Rivers then east along the Spanish Trail across the Mojave Desert (outside the assumed historic sage grouse range). But, north of Las Vegas, Fremont may have reentered the assumed historic sage grouse range again when he followed the Sevier River north to Utah lake, then across northern Utah, past the Uintah Mountain trading post of Antoine Robideau and eastward past Brown's Hole, Vermillion Creek and St. Vrain's Fork of the Green River and back to the valley of the Platte River once more (Goetzmann 1959, p. 100-101).

In 1845, three expeditions entered the West. Abert's expedition went through the Texas panhandle and may have entered or come near the panhandle sage grouse area and the intervening area in eastern Colorado, but the rest of his travels were probably too far south (near Albuquerque, NM and further south) to lie within the range of any sage grouse populations (Goetzmann 1959, p. 114, map). Lt. William B. Franklin recorded scientific observations on Abert's expedition (Utley 1997, p. 226). Kearney's expedition followed the North Platte and Platte Rivers to South Pass, and from Fort Laramie south along the front ranges to Bent's Fort area (Goetzmann 1959, p. 114, map). Fremont led another expedition through South Park, along northern Colorado and Utah to the Great Salt Lake and then across the northern Great Basin and across the Sierras to Sutter's Fort area (Goetzmann 1959, p. 114, map). Part of Fremont's party traveled southward along the eastern Sierras and crossed them at Walker's Pass area (Goetzmann 1959, p. 114, map). In 1846, Emory's expedition also passed through the area between the known Colorado sage grouse populations and the panhandle sage grouse populations when they traveled south along the Front Range from Bent's Fort through Colorado and New Mexico and then west across the pass to Santa Fe area (Goetzmann 1959, p. 114, map). In 1849, Simpson and Marcy also passed through Texas panhandle following the course of the Canadian River (Goetzmann 1959, p. 215, map). In 1850, Stansbury followed the emigrant trail along the Platte River to South Pass and then to Fort Bridger and along the eastern shore of the Great Salt Lake to Fort Hall. He returned along the western shore and Pilot Peak and passed near Salt Lake City, and then traveled south of the regular emigrant trail through the Red Desert area of Wyoming to reach Fort Laramie (Utley 1997, p. 267). Baird and Girard prepared a Zoological Report from Stansbury's expedition that included a list of all the trans-Mississippi birds not included in Audubon's American Ornithology (Goetzmann 1959, p. 225). Also in 1849, Warner and Williamson crossed out of the Central Valley in California via Madeline Pass, across the Lassen and Modoc plateau area to Goose Lake (Goetzmann 1959, p. 251-253). This area was one of the

more southerly areas containing the Western sage grouse. In the northern portion of the historic range, Warren undertook expeditions in 1855, 1856, and 1857, and other expeditions were made by Raynolds and Mullan (Goetzmann 1959, p. 408, map). The Raynolds party included a number of scientists, among them F. V. Hayden (Utley 1997, p. 279). Joseph Leidy, then at Univ. Penn., analyzed the collections from Warren (Goetzmann 1959, p. 412).

The Topographical Corps undertook a series of more specific railroad surveys following the passage of the Pacific Railroad Survey bill in 1853 (Cong. Globe, 32nd Cong., 2d Sess., 26, 841). Expert scientists accompanied each survey or reconnaissance party to collect natural history observations and specimens (Goetzmann 1959, p. 275). The surveys of Stevens, McClellan, Williamson, Beckwith and Gunnison all passed through the historic range of sage grouse (Goetzmann 1959, p. 276, map). In several cases, the parties traveled far from the survey line eventually agreed upon. For example, elements of the Stevens expedition ranged far over the entire Northwest (Goetzmann 1959, p. 281).

After the railroad surveys, the Topographical Corps undertook surveys of wagon road routes, and the Simpson survey for the Minnesota to Reno road, the Bryan survey from west Texas to the Rockies, and, possibly, the Macomb survey in north central New Mexico passed through the historic sage grouse range (Goetzmann 1959, p. 349, 362-370). In 1859, Captain H. D. Wallen surveyed a route for a wagon road from The Dalles, OR to Camp Floyd in Utah. Wallen's party journeyed southeastward from the Deschutes River to Lake Harney, and then along the Malheur River and on to Old Fort Boise. The party also explored the route of the Owyhee River (Goetzmann 1959, p. 356). In 1853, McClellan surveyed a road from Fort Steilacoom to Walla Walla (Goetzmann 1959, p. 357). Simpson's survey traveled from Fort Bridger across central Nevada to Lake Tahoe, and in 1859 Macomb traveled northwest from Santa Fe to penetrate the Four Corners area and Great Sage Plain east of the junction of the Green and Grand Rivers (Goetzmann 1959, p. 85, map). Simpson's report was not published until 1875 but included a complete survey of the botany and zoology of the region he surveyed. Further expeditions ceased during the Civil War, and the Corps was ultimately disbanded. The last survey established the Canadian boundary and was led by Lt. J. G. Parke between 1857 and 1861. George Suckley described the avian specimens from the survey. The final report was lost but the field reports and monographs are held in the National Archives (Goetzmann 1959, p. 428-429).

Trappers continued to explore the West during the era of the Topographical Corps, as well as to lead some of the Corps' surveys and immigrant wagon trains. Others also explored the West during this period, including some European scientists. For example, the German scientist H. B. Mollhausen traveled with both the Duke Paul of Wurtemberg's Rocky Mountain expedition as well as with Whipple's survey party (Goetzmann 1959, p. 310). Others included the botanist Creuzefeldt, and Marcou, a protégé of Agassiz (Goetzmann 1959, p. 310). Apparently some collected specimens and perhaps some sage grouse specimens made their way to museums in Paris, Potsdam, Leipzig, and London (Goetzmann 1959, p. 311). The painter Karl Bodmer traveled with the expedition organized by the German prince Maximilian on a tour of the upper Missouri River in 1833-34 (Utley 1997).

Accounts of Others

The first trained naturalist to travel overland from the Rocky Mountains to the west coast was Townsend (1839). In 1834, Townsend traveled through the Green River valley and reported

that sage grouse flushed by the hundreds in front of his horse. Vale (1975) compiled information from 29 journals and diaries to elucidate the extent of sagebrush and grass areas in the Intermountain West. Christensen and Johnson (1964) compiled early accounts for some of the valleys in Utah. Analyses of accounts by Oregon Trail travelers, early settlers and travels by scientists and natural historians prior to the 1920s for information on sage grouse might prove fruitful. Mormon pioneers are known to have consumed "prairie hens" during their wanderings (Kimball 1988). The Smithsonian Institution has 138 sage grouse specimens in their collection, which constitute their entire holding for this species (Ludwig 2001). Braun and Schroeder have previously examined these specimens, but not all the notebooks and expedition accounts.

Settlement and Degradation

The sagebrush shrub-steppe was one of the last areas of the conterminous United States to be explored or settled (Cline 1963). It was not until 1844 that Fremont concluded that the Great Basin did not drain into the Pacific or the Gulf of Mexico (Jackson and Spence 1970). The huge numbers of sage grouse were a result of the vast expanses of habitat. In Idaho, early settlers described vast "seas of wormwood" stretching as far as the eye could see (Quinney 2000, p. 91). Pioneers described a diverse sagebrush, forb and grass ecosystem – the expanses of sagebrush appeared like "a field of wheat" because of the tall rye grass stems protruding above the sagebrush (Quinney 2000, p. 91). Balsamroot (*Balsamorhiza* spp.) was the most commonly noted forb, and was so abundant that "mile after mile" of the sagebrush lands were colored yellow every spring (Quinney 2000, p. 91).

Despite the efforts of naturalists and the Army Topographical Corps, Historian Daniel Boorstin's aphorism that the West was "settled before it was explored" (Goetzmann 1986, p. 178) is particularly apt for sage grouse distribution and numbers. Rapid habitat degradation led to severe declines in the millions of sage grouse, and these declines continue. Initially, degradation was highly localized and limited to the corridor of the Oregon Trail and other major trails, and in the vicinity of established forts. Oregon Trail users so heavily depleted the vegetation that they had to drive their livestock several miles away from the trail corridor to get enough forage (Quinney 2000, p. 92). In the early 1900s, sagebrush ecosystems rapidly became subject to settlement and grazing, and, after WWII, to industrialized agriculture. But, in the late 1800s and even into the 1920s, sage grouse were locally abundant. In parts of northern Nevada, sage grouse "clouded the sky" and boys were able to kill sage grouse by reaching out and hitting them with a stick (Wuerthner 1999). Huge bands of sheep destroyed nesting habitat, and hunters shot so many sage grouse that "a dead-axle wagon wouldn't hold the birds they killed," so the hunters "would just leave [them] on the ground in big piles to rot (Wuerthner 1999). In parts of Idaho, whole wagonloads of sage grouse were shot by hunters (Scutro 1999). In Colorado, sage grouse were found in the eastern plains, at least as far as 25 miles NE of Ft. Collins as late as 1949 (Bailey and Niedrach 1965, p. 279).

As late as 1858, white occupation of Montana was limited to a few forts clustered around the confluence of the Marias and Teton rivers with the Missouri river (Utley 1984, p. 25). Nor had any settlements penetrated deeper into the Intermountain West than Ft. Laramie in present day Wyoming and two forts east of the Rio Grande in present day New Mexico (Utley 1984, p. 62). Shortly thereafter, forts and towns were established at several places within the range of the sage grouse (Utley 1984, p. 121, 194-95).

After a series of wars, skirmishes, massacres, expatriations, ethnic cleansings and genocide, many native nations collapsed and remaining Indian tribes and bands were largely limited to small reservations (Utley 1984, p. 233). Native Americans had become ineffective as an ecological force, and the West, including the range of the sage grouse, was opened to white settlement and agricultural uses. In 1874, J. F. Glidden invented barbed wire, providing a cheap and effective means for containing livestock, which also led to the elimination of the long drives of cattle to railheads and the death of the cowboy as anything more than a mythic figure. The extension of railway lines and invention of the refrigerated railway car opened western cattle operations to markets in the east, notably Chicago (Cronon 1991) and began the agro-industrialization of the West. By 1890, the Superintendent of the Census had declared the frontier dead, as Frederick Jackson Turner noted in his 1893 lecture explaining wilderness and frontier as effects shaping the American social and psychological character (Turner 1921). Farming and settlement accelerated during and just after World War I, when many homesteaders filed Desert Land Entry claims because of the demand for grain (Quinney 2000, p. 93). Many of the farms and ranches in the semi-arid and arid lands of the plains and cold deserts failed during the dust bowl years, and cheatgrass (*Bromus tectorum*) rapidly invaded the disturbed lands (Quinney 2000, p. 93). Later, especially during the 1940s and 1950s, increasing industrialization of the West began. As late as the 1960s, large tracts of sagebrush (although degraded by grazing and cheatgrass infestation) still existed south of present day Interstate 84 (Quinney 2000, p. 91). Habitat conversion – fostered by cheap irrigation water – increased rapidly in the 1970s following completion of the upper Snake River dams. In the 1980s, the next wave of habitat destruction became prominent – the increasing proliferation of suburbs, exurbs (Davis, et al. 1994), and ranchettes. Thus, in the space of a few decades, the vast prairies and shrublands of the west were rapidly converted from natural areas dominated by buffalo, prairie dogs and sage grouse into agro-ecosystems dominated by sheep and cattle, into industrial landscapes dominated by mines, pipelines, powerlines, and roads, and into suburban sprawl.

Patterson (1952c) estimated that the pre-settlement area of habitat for sage grouse was about 90 million acres (36.4 million ha, or 140,625 mi^2) in 1952, with another 40 million acres (16.2 million ha) of less suitable habitat also available. Braun used earlier accounts of sage grouse and habitat estimates to approximate the historic numbers of sage grouse as about 2 million (Braun 2001c). However, applying contemporary density estimates to the known pre-settlement range suggests total numbers that are much larger. For example, if the 12.5 males/$mile^2$ estimate of Patterson (1952c) is multiplied times 2 to account for adult females, and then by the 140,625 mi^2 of the best habitat, a total of 3.5 million adult birds is obtained. If the estimate of Edminster (1954) is used, if Patterson's value of 40 million acres of less suitable habitat is added, if spring populations are used, if more than 1 female is assumed for every male, if density estimates higher than the contemporary ones are used (recognizing that all habitat has been degraded), or if it is recognized that sage grouse were already in decline at the time Patterson and Edminster estimated densities, then it is clear that a pre-settlement estimate of several million birds is quite conservative. Pre-settlement North America may well have contained over ten million sage grouse. Certainly, there were formerly millions of sage grouse in North America.

Historic Range of the Eastern Subspecies

Historically, the Eastern subspecies extended eastward from its border with the Western subspecies and penetrated eastward about one-third of the way across North and South Dakota, and into northwestern Nebraska (Schroeder 2000a). Across these longitudes, they ranged through all sagebrush areas from southern Canada into northern New Mexico and Arizona. Sage grouse also occurred in a disjunct area near the Oklahoma pan handle. These are likely to have been Gunnison sage grouse, but that will never be known, as they are extinct.

Present Range

Today, sage grouse have been extirpated from 5 states and the Canadian province of British Columbia (Schroeder, et al. 1999a; IUCN Red Book 1999), and are sparsely and locally distributed from southeastern Oregon, southern Idaho, and southern Alberta and Saskatchewan south to eastern California, and eastward through Montana, Wyoming, Utah and Idaho to western Colorado, and extreme western North and South Dakota. Extinction in "imminent" in Alberta, and "only 6 leks" remain (Boyce; personal communication, June 26, 2000). The range of the species has been reduced in every state (Schroeder, et al. 1999a). Using the GIS data on which Schroeder (2000a) based his map, sage grouse of all species, subspecies, and distinct population segments currently occur in only 170 counties in the U.S., a reduction of about 40% from the 271 counties in which the bird occurred historically. A large number of isolates have appeared where once there were continuous populations – e.g. 2 in Washington state, and numerous isolates in Colorado, Nevada, and California (Schroeder 2000a). Fragmentation has produced isolation within this range, and sage grouse within the above delineated area cannot be assumed to form a single population. Nor can all the sage grouse within any state be assumed to form a single population. Severely isolated populations of the Western sage grouse occur in California, and in eastern Washington (Johnsgard 1983, National Geographic Society 1987, Wallestad 1975a).

Sage grouse have been extirpated in British Columbia, most of North and South Dakota, Nebraska, Kansas, Oklahoma, Arizona, New Mexico, much of Oregon, most of Washington, and central eastern California (Hamerstrom and Hamerstrom 1961; Ihli, et al. 1973; Schroeder 2000a). Thus, great contractions in the range have occurred, and other than a few remnant isolates, birds remain only in parts of Wyoming, Idaho, Montana, Oregon, Nevada and Colorado. However, populations are fragmented in these states as well, and "the species is depleted throughout most of its range" (Oregon Dept. Fish and Wildlife 1991).

In 1992, BLM estimated that 30 million acres of habitat on BLM lands were occupied by sage grouse but that another 10 million acres of habitat were unoccupied (BLM 1992, p. 5-6). This is far below the estimate of 130 million acres of total occupied habitat pre-settlement (Patterson 1952c). Most habitat is on BLM lands today, so if both estimates are correct, then about 90 million acres of habitat have been lost on private lands. BLM stated that these "declining populations trends are likely to continue" without changes in management (BLM 1992, p. 6). Yet BLM has not changed its management.

Sage grouse are undergoing a "range collapse" – a "rapid contraction[] of [a] once widespread species to one or a small number of isolated sites (Brown, et al. 1996, p. 612). This process is highly advanced in the Gunnison species, well developed in the Western subspecies, and common in the Eastern subspecies (see Schroeder 2000a). Range collapse present in all sage

grouse taxa is "distinct from the incremental expansions and contractions" that normally occur at the edges of the range for most vertebrates (Brown, et al. 1996, p. 612). Additionally, the perimeter to area ratio of the range is increasing in sage grouse (see Schroeder 2000a). In most species, the perimeter to area ratio of the range is nearly constant (Rapoport 1982; Brown, et al. 1996, p. 608). This change in perimeter to area ratios is driven by fragmentation and greatly decreases population viability. Many inhabited areas of the range have been split from the intact range and populations in those areas have gone extinct. Other inhabited areas have been separated from the intact range more recently, but sage grouse are likely to be extirpated in these areas soon. Holes and long, "fingers" or invaginations have opened up in the range causing disjunct populations that are ripe for extinction. The process in which these finger-like areas are created from formerly intact habitat has been termed "habitat shredding" (Feinsinger 1997). In such long, linear areas, edge effects and interactions with the components of adjacent areas are of paramount concern (Forman and Godron 1986). Both the finger formation process and gap formation from perforation of the landscape matrix by holes are well-known stages in fragmentation processes (Meffe and Carroll 1997, p. 278). Importantly, there are "no source populations of sage grouse" anywhere within the range, and "all studied populations of sage grouse have been in decline for at least 40-50 years" (Braun 2000e). Worse, experts "know of no sage grouse range expansion anywhere, ever" (Braun 2001b). An Idaho Fish and Game biologist echoes this assessment: "There are no areas over the range of sage grouse that have shown a population increase or even stable populations over the last 30 years" (Reese 1998). Thus, the range consists solely of population sinks, which will perish as dispersal is reduced.

Even within their existing range, numbers have declined dramatically and these declines are ongoing (Braun 1998a; Connelly and Braun 1997; Wisdom, et al. 1998). Populations are now disjunct, sporadic in occurrence, and thinly distributed across the landscape. Braun (1993) considered birds remaining in North Dakota, South Dakota, California, Colorado, Utah, Washington, Alberta and Saskatchewan to be "marginal" or "greatly reduced." For continuity, some present day extirpations and population declines are noted above, under relevant sub-sections of the Historic Range and Early Accounts sections.

Present Range of the Eastern Subspecies

The huge swath of sage grouse habitat which formerly stretched across North America is gone now. As shown in Schroeder (2000a), the Eastern sage grouse is split into 3 main geographic ranges or groups. The 3 groups are separated by large areas of habitat destruction in southern Idaho and northern Utah, and groups 1 and 3 are also separated by areas in western Montana. (1) the western-most range includes the southeastern corner of Oregon, northern Nevada, and the southwestern portion of Idaho. (2) In central Idaho and western Montana, a cluster of fingerlike projections of remaining habitat harbors another range of sage grouse, with two islands of habitat occurring south of that in southeastern Idaho and part of northern Utah. (3) The eastern-most range extends through parts of western Montana, Wyoming, eastern Utah, and northern Colorado. In the near future, this group will likely split into two more disjunct ranges in the area of Crook, Campbell, and Sheridan counties in Wyoming, and Carter and Powder River counties in Montana. Invagination of the range in this area is already advanced, and habitat conversion continues. Thus, both large scale and small scale fragmentation will further reduce sage grouse range.

The range map prepared by Schroeder (2000a) was based on earlier data, much of it quite spotty, and may be out of date by now. Thus, the range is likely smaller and more fragmented than discussed above, particularly because very large and hot fires have destroyed sagebrush in many parts of the West in the last few years.

Population Isolation

Of particular import for the assessment of population size, and hence viability, is the degree to which panmixis occurs across the landscape. If birds interbreed only between leks or small clustered groups of leks, then actual population sizes will be quite small. Various authors, particularly state and federal agency employees, have referred to the aggregate estimate of birds in an entire state as a "population." Although a tempting shorthand, there are no data to show that sage grouse do in fact form biological populations across an entire state. The use of the term population should be restricted to its biological meaning, otherwise, an overly optimistic misunderstanding of population viability is promoted, increasing the risk of extinction.

Many authors have found that hens are more likely to move between leks, while males are very site specific. Wallestad and Schladweiler (1974) observed complexes of leks and found that daytime movements were restricted to 0.8 to 1.1 miles from the strutting grounds. Of these movements, 82% exceeded 0.2 miles. Carr (1967b) found a similar pattern, observing that birds did not venture beyond 0.9 miles from the lek. Dominant males rarely move between leks (Johnsgard 1973, p. 164), and Dalke, et al. (1963) reported that in a two year study of 78 banded males and 107 banded females, only 6% of females and 18% of males were even observed present on lekking grounds other than where they were first banded. In the 2 year study, Dalke, et al. (1963) found that sage grouse showed great fidelity from the first year to the second year to the lek complex, but not to the lek itself. This suggests that unless lek complexes are adjacent to each other, the maximum size of sage grouse populations will be determined by the extent of the lek complex. Even this may overstate population sizes: in a previous study, Dalke, et al. (1960) found that 70% of banded birds did not change from one strutting ground to another, even over a several year period.

Sage grouse are unlikely to cross more than 6 to 8 miles of unsuitable habitat (NWEA 1999, p. 26; citing Braun, personal communication, and Connelly, personal communication). Even though they are capable of long distance movements, sage grouse "avoid[] areas without sagebrush cover" (Dunn and Braun 1986a). Since many landscape features such as roads, powerlines, reservoirs, and agricultural fields now subdivide sage grouse habitat, it is highly likely that the range now consists of a large number of isolated populations, rather than a large panmictic population or even a well-connected meta-population. The implications for extinction risk are enormous.

The best available scientific data indicate that sage grouse will tend to be isolated into separate populations unless continuous lek complexes occur across the landscape with no gaps exceeding about 2 miles. The type of gap will likely be important: degraded sagebrush habitat will no doubt be less of a barrier to movement, and hence gene flow, than expanses of agricultural fields, grasslands without shrubs, or powerlines. Johnsgard (1973) thought movements between leks to be rare.

Matings, and production of viable offspring would likely be much lower than these movement rates. Such movements, even if accompanied by matings, would not constitute

effective levels of gene flow unless impregnated females were able to raise viable offspring who could prevail during all life history stages and raise viable young themselves.

The fact that it is the young, inexperienced birds that are most likely to appear at multiple leks indicates that gene flow is probably small among different leks. These are precisely the males who are least likely to obtain matings, and the females who are least likely to successfully raise broods if they are mated. Moreover, if the sexual selection in this species is related to functional life history characteristics such as overwinter survival ability, ability to evade predators, and the like, then younger females or females mated by younger males that raise broods to maturity will still have lower fitness than more experienced females or those mated by more experienced males. Moreover, neither experienced males or experienced females show much movement among leks.

As with the movements among leks, yearlings are also the life history category that disperses the greatest distance (Dunn and Braun 1985). Females are more likely to disperse longer distances than are males, with yearling females being the life history category that disperses the longest distances (Dunn and Braun 1985). The fact that long movements are typically undertaken by reproductively naïve individuals increases the isolation of populations and creates much greater risk of extirpation. Sage grouse less than 2 years of age are less successful at hatching clutches and raising young than are older females (Braun 1995d, p. 2). Moreover, if sub-dominant birds are the major source of gene flow among demes, then the alleles that are introduced into these small sub-populations may well be deleterious ones, thus depressing mean population fitness and increasing the risk of extinction.

Habitat

Sage grouse are completely dependent on sagebrush-dominated habitats (Benson, et al. 1991). Sagebrush ecosystems are a little-loved landscape and have not received conservation interest in the past. Consequently, livestock grazing interests and other "special interest groups have successfully pressured.government agencies" to alter and degrade these ecosytems to the detriment of wildlife (Braun, et al. 1976). Many managers of the public lands have perceived these ecosystems to have "little value" (Braun, et al. 1976), making such co-optation even easier. Habitats at low elevations, in more southerly latitudes, and more arid environments have been most damaged over the last century, and many are now uninhabitable (Schroeder 2001a).

Sage grouse habitat needs vary somewhat with life history stage and, consequently, with seasonality. Braun (2001f) recently summarized these requirements. Sagebrush is a crucial component of the diet year-round (Johnsgard 1983). The range of the sage grouse contains about 12 species of sagebrush, many of which have numerous subspecies. When selecting cover, sage grouse rely almost exclusively on sagebrush (Johnsgard 1983, Howard 1996). Both federal and state agencies agree that declines in the abundance and range of sage grouse "relate to habitat loss, habitat degradation, and habitat fragmentation" (MOU 1995). Sage grouse habitat and cover requirements are inseparably tied to sagebrush, but sage grouse also require abundant forb cover. Before Euro-American colonization of the West, natural shrub-steppe "was probably composed of open stands of shrubs with a strong component of grasses and forbs in the understory" (Miller, et al. 1993, p. 115). Over 50% of sage grouse habitat has been eliminated (Patterson 1952c, p. 12). Moreover, there are no known areas of habitat that have not been degraded or destroyed by conversion to other uses, livestock operations, or "rangeland

treatments" (Braun 1998a). Reduction or elimination of grasses, cryptogamic crusts, and forb cover by livestock has deprived sage grouse of food and cover, and led to increased densities of sagebrush and juniper invasion (Tisdale and Hironaka 1981).

Although habitats shift with seasonal resources and aridity, generally speaking the best soils, best vegetation, and most critical habitat were in fertile valley bottoms with slopes of less than 10% (Cadwell, et al. 1997; Livingston 1998). These were the areas that were most rapidly converted to agricultural uses and are now often in private hands. In the Columbia Plateau of Oregon and Washington "agricultural conversion has been concentrated" in these "areas of deep, arable soils" (Altman and Holmes 2000, p. 11), and the remaining valley bottom lands are the second most impacted ecosystem type in the region (Altman and Holmes 2000, p. 4-5, 8).

Sagebrush with more than about 30% canopy cover may cause reduction in forb cover due to competition (GBCP 1997, p. 40). This may be of particular concern in the Gunnison Basin because grasses and forbs are under-represented in a large proportion of the sagebrush areas of the Gunnison Basin (GBCP 1997, p. 39). Management recommendations for sage grouse habitat are presented in several sources (Call 1979, Gunnison Basin Sage Grouse Conservation Plan, GBCP 1997, Appendix E), and by the Western States Sage Grouse Technical Committee (WSSGTC 1999). However, the conventional measures and derived indices of habitat suitability in those sources do not include many threats associated with landscape features, such as fragmentation, edge effects, or movement corridors (Schroeder 1998a). Worse, the guidelines are not based on purely scientific criteria; instead, they result from a politicized process in which a "series of compromises" were made to reduce specificity and get various state governments to sign on (Braun 2001a).

Sage grouse occur at elevations from 1,200 m to 2,400 m in Oregon, and above 600 m in Washington. In Colorado, the birds occur up to 2,900 m (9,500 ft.). Elevation, per se, is unlikely to be a limiting factor in sage grouse distribution; instead, the presence of suitable habitat is likely set by such factors as elevation, soil moisture, and temperature, with grouse distribution a concomitant of sagebrush distribution.

Historically, shrubs dominated the Intermountain West below tree line, and true grasslands were limited to moist valley bottoms, riverine areas, and some hillsides (Vale 1975). Sagebrush extended from somewhere between Casper and Ft. Laramie, Wyoming in a nearly unbroken sea to the slopes of the Cascades in central Oregon (Vale 1975). Sagebrush shrub-steppe is a structurally simple habitat (Bendell 1972a, Dasmann 1981). And, at least before the era of Euro-American settlement, that habitat occurred in large blocks (Rich 1985a, Fig. 1; Leopold 1933). Sagebrush shrub-steppe habitat has now been severely fragmented. Loss of habitat by conversion to agriculture and habitat degradation has been "severe" and "the future for remaining sagebrush steppe in particular is bleak" (Paige and Ritter 1999). Welch (draft manuscript, Ch. II, p. 12-14) reviews the degradation and destruction of habitat by land managers under the aegis of "vegetation control," comments on the problems, and summarizes recommendations. Grazing of livestock has severely degraded most of the remaining sagebrush habitat: 30% is "moderately" grazed ("moderate" means that only "remnants of native herbs" remain), and another 30% has been so heavily grazed that "the native understory [is] replaced by introduced annuals (Paige and Ritter 1999, p. 7; West 1988, 1996).

Ricketts, et al. (1999b) note that 14 of 16 temperate grassland-savanna-shrub habitat types in North America are either in critical danger or are endangered (p. 63, Table 4.2). This

includes virtually the entire range of sage grouse, and all of the range is listed as endangered, threatened, or vulnerable (Ricketts, et al. 1999b, Fig. 4.3). Of particular concern for the Wyoming Basin is the impending increase in energy and mineral development (Ricketts, et al. 1999a, 1999b; Sands, et al. 2000). The range of sage grouse contains little intact habitat (Ricketts, et al. 1999b, Fig. 4.2). Over 80% of this ecosystem type has been "substantially altered" by human activities (Hemstrom, et al. undated, p. 3; West 1999b). Other scientists – including the National Biological Service (now the Biological Resources Div. in the US Geological Survey) – have classified ungrazed sagebrush ecosystems as "critically endangered (> 98% decline)," their most endangered category (Noss, et al. 1995; Noss 1999b). Moreover, little of this region is now ecologically intact (Ricketts, et al. 1999a, Fig. 4.2), and virtually the entire range is threatened by invasive alien plant species (Ricketts, et al. 1999a, Fig. 4.4a, b).

Some habitat types appear to be used at all seasons of the year, and for all life history stages. For example, relatively dense, tall stands of sagebrush are used by all age classes for roosting (Drut 1994). Also, substantial forb and grass cover is required at all life history stages for both food and concealment. This point was recently emphasized by Crawford (1997). Topographically, anecdotal observations suggest that sage grouse prefer areas with good visibility, probably for predator detection. Schmidt (1998) suggested that a topographic break with a depressed swale was preferred.

Additional habitat needs are analyzed by life history stage, below. In these analyses, it is important to realize that the optima or the requirements found for sage grouse habitat represent joint probabilities. If optimal sagebrush canopy cover is found on a steep slope then habitat will not be optimal and may be unusable.

O'Connor (1986) has cautioned that it is unsafe to predict bird densities on simple linear, or even monotonic, habitat functions. Moreover, the mere observation that populations are abundant in an area cannot be used to justify an argument that habitat is adequate in that area (Van Horne 1983, O'Connor 1986). It is well known that crowding of individuals into remaining habitat patches occurs as habitat destruction or degradation takes place (Meffe and Carroll 1997, p. 290). Areas with relatively large or dense populations may not be productive habitats; indeed, such areas may be population sinks and may disappear if immigration is interrupted by fragmentation effects (Pulliam 1988). Such areas may also be attractive to individuals, yet not able to survive there because of predation or other effects, thus serving as an "ecological trap" (Gates and Gysel 1978, Ratti and Reese 1988). Thus, investigators may "easily be misled about the habitat requirements of a species" (Pulliam 1988, p. 659). Habitat analyses must include measurements of productivity, not merely density counts. Moreover, temporal fluctuations in environmental factors can change former source habitats into sinks – this is an important concern in areas subject to climatic variation and global warming.

Although nearly all analyses reviewed below assume that habitat selection is an optimizing process, many environmental factors and behavioral cues have changed as a result of anthropogenic effects. In a similar "flat" or 2-dimensional habitat (tall grass prairie), Johnson and Temple (1986) demonstrated that birds failed to select high quality nest habitats. Instead, birds chose habitats yielding lower nest productivity. Because sage grouse occupy similarly flat habitats, it cannot be assumed that they select the best quality habitats, and management actions must not focus only on areas near nests nor on areas that already contain the greatest numbers of birds.

Roosting often takes place on rocky outcrops (Crawford 1960, Dalke, et al. 1963) as well as ravines, stream bottoms, and tall sagebrush (Johnsgard 1983). In winter, sage grouse will burrow into snow (Patterson 1952c; Beck 1977; Hupp 1987d; Back, et al. 1987). Similar behavior is common in other grouse, birds and mammals because the sub-nivean environment is often less harsh than above-snow conditions.

Degradation of habitat is a significant risk factor throughout the range of the species (Braun 1999a, p. 1). The quantity of habitat, which is related to the geographic range, has been reduced so significantly that it too is a significant risk factor throughout the range of the species. Habitat requirements have been synthesized in a number of works (summary in Connelly, et al. 2000e) and simple habitat usage models have also been constructed (Ramsey, et al. 1994).

Beyond the amount and composition of habitat, it is now well known that the pattern in which habitat is arranged across the landscape, the spatial distribution of habitat, is an important factor in extinction rates and dynamics (Shaffer 1997). This issue is discussed more thoroughly in other sections of this review, with a synopsis in the Habitat Fragmentation section and its subsections.

Plant Associations

Sage grouse are obligate residents of the sagebrush (*Artemisia spp.*) ecosystem, usually inhabiting sagebrush-grassland communities. Sage grouse are rarely found far from sagebrush (Drut 1993). Much of what is termed sagebrush-steppe consists of areas where bunch grasses are co-dominant with sagebrush (West 1996). These areas occur mainly in Oregon, Washington, Idaho, Montana, and Wyoming (Paige and Ritter 1999, p. 3, map). Further south, in Nevada, Utah, southern Colorado, and northern New Mexico and Arizona (Paige and Ritter 1999, p. 3, map), sagebrush becomes the sole dominant (West 1996). Rhizomatous grasses occur further east in sage grouse habitat in the Great Plains. This dominance refers to potential natural vegetation – livestock grazing and "vegetation control" have removed most grasses and forbs from huge expanses of landscape. Meadows surrounded by sagebrush may be used as feeding grounds (Johnsgard 1973). All sage grouse are habitat specialists on sagebrush.
A substantial scientific literature exists on sagebrush. A bibliography with over 1,250 citations has been published by Harniss, et al. (1981), and Tisdale and Hironaka (1981) have reviewed much of the sagebrush literature. Numerous more recent references are found in Webb and Salvo (2001). Distribution of sagebrush, juniper, and other shrub and tree species across edaphic gradients is presented in Thompson, et al. (1999). In preparation is a large monograph on sagebrush (Welch, manuscript chapters).

Sage grouse occur across several different climatic zones, two sagebrush ecosystem types (sagebrush steppe and Great Basin sagebrush types), several geographic subdivisions of sagebrush types, and ecosystems with multiple plant associations (Miller and Eddleman 2000, p. 1). For convenience, this review will use the term sagebrush or sagebrush shrub-steppe to refer to the range of sage grouse sagebrush habitat in its entirety, and the more specific terms for the two different sagebrush ecosystem types, or the various plant associations, physiographic regions, cover types or climatic zones as defined in this section. Maps showing the extent of climatic regions, both sagebrush ecosystem types, and the geographic subdivisions of the sagebrush biome are presented in Miller and Eddleman (2000, p. 4-5, figs. 1-2). Wyoming big sagebrush communities are the most extensive and most arid of the sagebrush community types

(Miller and Eddleman 2000, p. 21). This community type is "probably in poorer condition across its range than more mesic sagebrush types" (Miller and Eddleman 2000, p. 21). Thus, the most widespread sagebrush type is in the worst condition. Most non-eroded sagebrush steppe soils are Xerolls (drought affected Mollisols) and most sagebrush semi-desert soils are Aridisols (West 2000).

Sagebrush ecosystems may be analogized to forests in their vegetative structure. Sagebrush and other brush species form the canopy and various grasses and forbs from the understory. Two differences exist: grasses often reach into or above the sagebrush canopy, and human caused damage to this ecosystem has mainly been to the understory, rather than to canopy species (as with logging of old growth forests). The most common grasses are wheatgrass (*Agropyron* spp.), an introduced species, various fescues (*Festuca* spp.), bluegrasses (*Poa* spp.), introduced bromes (*Bromus* spp.), junegrass (*Koeleria* spp.), needlegrasses (*Stipa* spp.), ricegrassses (*Oryzopsis* spp.), and wildrye (*Elymus* spp.). A great variety of forbs (wildflowers) are present, but one species, arrowleaf balsamroot (*Balsamorhiza sagittata*), is widespread and abundant relative to other forbs. Other common forbs include Yarrow (*Achillea* spp.), pussytoes (Antennaria spp.), locoweed (*Astragalus* spp.), larkspur (*Delphinium* spp.), and daisy (*Erigeron* spp.).

The sagebrush steppe ecosystem type harbors about 250 species of terrestrial vertebrates (Sands, et al. 2000). Most of the vertebrate species are birds (100 species) or mammals (70 species) (Braun, et al. 1976). A "vast landscape of agricultural developments and nonnative grasslands" fragments the ranges of most vertebrates that were formerly common and abundant (Sands, et al. 2000, p. 27).

Most of the range of sage grouse was assigned to the Great Basin (11) and Rocky Mountain (19) biogeographic provinces by Udvardy (1975), whose classification scheme subdivided North America into 24 provinces. Sage grouse are associated with the following physiographic regions and plant cover types (Howard 1996):

BLM PHYSIOGRAPHIC REGIONS:

4 Sierra Mountains
5 Columbia Plateau
6 Upper Basin and Range
7 Lower Basin and Range
10 Wyoming Basin
11 Southern Rocky Mountains
12 Colorado Plateau
13 Rocky Mountain Piedmont
16 Upper Missouri Basin and Broken Lands

KUCHLER PLANT ASSOCIATIONS:

K024 Juniper steppe woodland
K038 Great Basin sagebrush
K055 Sagebrush steppe
K056 Wheatgrass-needlegrass shrub-steppe

SRM (RANGELAND) COVER TYPES:

107 Western juniper/big sagebrush/bluebunch wheatgrass
314 Big sagebrush-bluebunch wheatgrass
315 Big sagebrush-Idaho fescue
316 Big sagebrush-rough fescue
320 Black sagebrush-bluebunch wheatgrass
321 Black sagebrush-Idaho fescue
324 Three-tip sagebrush-Idaho fescue
405 Black sagebrush
406 Low sagebrush
407 Stiff sagebrush
408 Other sagebrush types
612 Sagebrush-grass

SRM 107 and Kuchler type K024 will not be suitable sage grouse habitat because juniper trees serve as raptor perches. These ecosystem types have expanded into the range of sage grouse. Orians (1993) criticized the lack of a single ecosystem classification scheme for vegetation type mapping; however, that should not be a problem for sage grouse habitat mapping, as sage grouse habitat will include all areas of sufficient size with a sagebrush overstory and with adequate forb and grass understory that do not have threats located in them.

Sage grouse formerly occurred throughout the range of big sagebrush (*A. tridentata*), except on the periphery of big sagebrush distribution or in areas where it had been eliminated (Call and Maser 1985). Three subspecies of big sagebrush dominate the sagebrush zone. These are basin big sagebrush (A. *t. spp. tridentata*), Wyoming big sagebrush (*A. t. ssp. wyomingensis*), and mountain big sagebrush (*A. t. ssp. vaseyana*) (Wright, et al. 1979, p. 2). Sage grouse prefer mountain big sagebrush and Wyoming big sagebrush communities, to basin big sagebrush communities (Cronquist, et al. 1984; Cronquist 1994). In most areas, big sagebrush communities lie at lower elevations than juniper woodlands or pinyon-juniper zones (Wright, et al. 1979, p. 1). Where these tree types are absent, other forests, such as ponderosa pine, curleaf mahogany, Douglas fir, Gambel oak, or lodgepole pine border sagebrush communities at their upper elevational limit (Wright, et al. 1979, p. 1). Pinyon-juniper woodlands often lie below sagebrush communities in the Great Basin (Wright, et al. 1979, p. 1). Sagebrush communities are heavily invaded by juniper and cheatgrass.

Sagebrush cover types other than big sagebrush can fulfill sage grouse habitat requirements. Sage grouse in Antelope Valley, California, for example, use black sagebrush (*A. nova*) cover types more often than the more common big sagebrush cover types (Schneegas 1967). However, it is unclear whether this use of black sagebrush was because nearby big sagebrush areas were degraded or represents a true preference for black sagebrush. Sagebrush communities not included in SRM cover types (Howard 1996) but supporting sage grouse include silver sagebrush (*A. cana*) and fringed sagebrush (*A. frigida*) (Rasmussen, et al. 1938; Wallestad, et al. 1975). Sage grouse use of less common sagebrush communities (i.e., Bigelow sagebrush [*A. bigelovii*]) may occur but is not documented in current literature. Franklin and Dyrness (1973, p. 216-222, 234-242) describe northwestern sagebrush communities.

Estimates of the historical range of sagebrush vary. Beetle (1960) mapped big sagebrush, and estimated its original extent as 79.3 million hectares (ha), which equals 196 million acres, and the range of all sagebrush species as 109 million ha (269 million acres). Campbell and Harris (1977) estimated that big sagebrush (*Artemisia tridentata*) originally dominated over 36.4 million hectares, and Miller, et al. (1986) estimated that in the 1980s it dominated 36.5 million hectares. Some authors have suggested that sagebrush has expanded, but those who have examined this assertion closely disagree, believing instead that sagebrush range has contracted (Welch 1999). Rephotography projects, which compare photographs from the 1800's with those taken from approximately the same vantage points in the late 20th Century, do not show any significant expansion of sagebrush (Klett 1984). Instead, rephotograhic analyses show increased mining development (Klett 1984, p. 16), juniper incursion (Klett 1984, p. 16, 138), reservoirs (Klett 1984, p. 54-55, 106, 107), ORV tracks and roads (Klett 1984, p. 94, 102, 121, 154-155), suburban developments (Klett 1984, p. 98-99), fencing (Klett 1984, p. 103, 136, 137), utility poles (Klett 1984, p. 104), and habitat conversion (Klett 1984, p. 128, 129). These analyses thus graphically depict many of the threats to sage grouse that have been erected during Euro-American settlement (Klett 1984).

Livestock grazing has been suggested as an agent in increasing sagebrush range, but more recent studies show that this is not supported (Peterson 1995). Similarly, Vale (1975) found no increase in sagebrush range. "If anything, the rate at which sagebrush lands are lost is increasing in recent years" (Knick 1998). Moreover, declines in sagebrush may be masked by expansion of juniper/sagebrush associations (Altman and Holmes 2000, p. 39). Miller, et al. (1993, p. 102, Fig. 1) present a map of sagebrush steppe and Great Basin sagebrush semi-desert, and cite Kuchler (1970a) for areas of 44.8 million ha and 17.6 million ha respectively (totaling 62.4 million ha). Miller and Eddleman (2000, p. 2) cite West (1983a, 1983b) for a similar figure, 62.7 million ha. Another range map of sagebrush is presented in Nelson and Tiernan (1983, Fig. 1), but does not show the topographically induced fragmentation of sagebrush range in Nevada. Comparison of the range map of Nelson and Tiernan (1983) with that of Miller, et al. (1993) shows that sagebrush has been extirpated from nearly all of eastern and central Montana, from most of eastern and northeastern Wyoming, Nebraska and the Dakotas, from northern Washington and from central and northeastern Oregon, and has retracted eastward from parts of California.

A number of vegetation classifications have been offered for sagebrush ecosystems. McArthur and Ott (1996) favored the Kuchler (1964a, 1964b, 1970a, 1970b) classification over Bailey's because the Kuchler approach defines vegetation types on a finer scale. Kuchler's classification scheme remains the only assessment of major above-ground ecosystem diversity describing the entire United States in reasonable detail (Crumpacker, et al. 1988), although that may change in a few years. The amount of land in the two sagebrush dominated Kuchler associations was quantified by McArthur and Ott (1996) and West (1983a, 1983b) for each state. Crumpacker, et al. (1988, p. 111) present a breakdown for various federal land management agencies – not surprisingly, BLM manages 75% to 83% of sage grouse potential habitat and USFS manages about 9%. USGS employees believe that Kuchler's (1964a) map "probably represents the best approximation available today of the continent's vegetation before European settlement" (Loveland and Hutcheson 1995).

Importantly, Kuchler's classification and others are based on potential natural vegetation, not on the actual vegetation present currently. Kuchler's map thus does not delineate original from natural vegetation or include disclimax communities formed by disturbance effects (Loveland and Hutcheson 1995). Kuchler's map and other similar ones are thus "little more than informed guess as to what might be" present as vegetative communities on the ground (Scott, et al. 1987; Botkin, et al. 1984). Potential vegetation is "far removed from what actually occurs on an area" currently and "provides little guidance" as to habitat quality and biodiversity protection (Scott, et al. 1989, p. 85). Perhaps the first comparison between Kuchler's potential natural vegetation and extant plant communities was that of Klopatek, et al. (1979), which used data valid to 1967.

Remote sensing has also been used to estimate extant vegetation types and land uses. The most recent coarse level vegetation maps are from a 1990 USGS dataset, interpreted from the Advanced Very High Resolution Radiometer; however, radiometry data are nonetheless quite coarse (Loveland and Hutcheson 1995). That study did not include urban areas, but urbanization data are available from the Defense Mapping Agency (Loveland and Hutcheson 1995). Other classification schemes have been developed, for example the USFS's ecoregions (Bailey 1976), and the Nature Conservancy's National Vegetation Classification System (M. Anderson, et al. 1998; Grossman, et al. 1998), which uses a hierarchical classification system with over 4,100 plant associations, recognized at the lowest level of hierarchy. However, remote sensing is unlikely to be able to resolve the degree of degradation of sage grouse habitat, particularly in the understory grasses and forbs that are so critical for reproduction and predator evasion.

For sage grouse habitat analysis, the area dominated by sagebrush is less important than fragmentation effects, and amount of area containing sufficient sagebrush, forbs, and grasses for good habitat. Proximity analysis (termed adjacency analysis by Mladenoff 1997) is also important – areas without sagebrush are used for feeding so long as they are near enough to sagebrush (or perhaps other bush types), which can function as cover for escape from predators. Such analyses are easily done using GIS (ASPRS/ACSM/RT 1992). Conversely, sagebrush dominated areas will not be adequate habitat if they contain juniper, pinyon, or other trees serving as raptor perches. In parts of Colorado, habitat has been invaded by Gambel oak (*Quercus gambelli*) (Commons 1997). Virtually all scientists working on sage grouse agree that habitat has greatly contracted, and has become increasingly fragmented (discussed further below).

Winter Habitat

Winter habitat is often the most limited seasonal habitat needed by sage grouse (Patterson 1952c, Eng and Schladweiler 1972, Beck 1977). The best winter habitat is below snowline, on flat or gently sloping south or west facing areas, where sagebrush is available all winter (Edminster 1954, Rogers 1964, Schneegas 1967, Jarvis 1974, Beck 1977, Autenrieth 1981, Martin 1976, Hupp and Braun 1989b). However, these are precisely the areas threatened by habitat conversion or already converted to agricultural fields (Miller and Eddleman 2000, p. 20). Moreover, in some areas only half the land surface is usable by sage grouse because of snow depth, slope, or disturbance to sagebrush (Beck 1977). Snows can drastically reduce available habitat. Wallestad noted that 12" of snow restricted sage grouse to only 7% of their winter

habitat (Eustace 1995), and Beck (1977) found that the birds were restricted to less than 10% of available habitat.

Birds exist exclusively on sagebrush during the winter, and it is relatively nutritious (Edminster 1954; Welch, draft manuscript, ch. II). Tetraonids may select for winter foods on the basis of secondary plant defensive compounds rather than proximal nutritional content (Bryant and Kuropat 1980). Birds typically forage in the tallest sagebrush (over 25 cm high) with the greatest canopy cover (more than 15%) (Wallestad and Schladweiler 1974, Beck 1977, Autenrieth 1981, Schoenberg 1982). Herein are reported the findings of primary research as given by the original authors, usually wildlife biologists. Some cover measures appear unusually large and may have been obtained using different methodologies than are typically used by plant ecologists. Dalke, et al. (1963) reported that wintering grounds of sage grouse in Idaho were usually located where snow accumulation was less than 6 inches (15 cm). Deep snow restricts the use of various areas and sage grouse winter where sagebrush has grown above the snow level (Dalke, et al. 1963; Autenrieth, et al. 1982; Hupp and Braun 1989b). As snow begins to accumulate, sage grouse are restricted to areas that support taller, denser sagebrush stands, such as south facing slopes. Damage or removal of sagebrush in such areas could severely impact all sage grouse populations because other areas may be buried by snow. These concerns apply to all sage grouse and have been raised in particular for Gunnison sage grouse in the Gunnison Basin (GBCP 1997, p. 40). Adequate winter habitat is also unavailable for Gunnison sage grouse in parts of the San Miguel Basin (SMBCP 1998, p. 4).

Snow cover that exceeds one foot in depth tends to force sage grouse into areas with taller sagebrush (> 16 inches) in valleys and lower elevation flat areas, and roost in shorter sagebrush along ridge tops (GBCP 1997, p. 4). In periods of extreme cold and deep snow, sage grouse often spend the night and portions of the day burrowed into snow drifts (GBCP 1997, p. 4-5).

Flock sizes in winter vary widely from 15 to over 100 birds, and flocks are often unisexual (GBCP 1997, p. 5). Flocks of males tend to be smaller than those of females. By early March, flocks are usually found within 2 to 3 miles of breeding areas (GBCP 1997, p. 5).

In winter and throughout the year, sage grouse select areas of little or no slope. Autenrieth (1986) found that birds selected areas of less than 15% slope. In a Colorado study of an area of 500 square miles (1,252 km^2) of sagebrush, nearly 80 percent of sage grouse winter use was on less than 35 square miles (87 km^2): on flat areas where sagebrush projected above the snow, or on south- or west-facing sites of less than 5 percent slope, where sagebrush was sometimes quite short but still accessible (Johnsgard 1983, Howard 1996). In Montana, during a winter with light snow cover, wintering areas were large flat expanses of dense sagebrush (Eng, et al. 1973). One study found that sage grouse selected wintering areas with slopes greater than 5□, probably because of the severe winter with greater than average snow depths occurring in that study (Hupp 1987b).

Winter home ranges of 5 females in Montana varied from 2,615 to 7,760 acres (1,058-3,140 ha) during two different years (Eng, et al. 1973). Robertson (1991) found winter home ranges exceeding 140 km^2 (53 $mile^2$).

Beck (1977) and Schoenberg (1982) found that birds used only 10% of winter areas selectively. Such high concentrations of birds exposes them to both predators and disease transmission, and points up the greatly reduced amount of habitat available (Drut 1994). Birds

select wintering areas with about 20% sagebrush canopy cover (Eng and Schladweiler 1972; Wallestad 1975a; Braun, et al. 1977; Autenrieth 1986). Aspect has also been found important for wintering areas, with birds selecting south or west facing slopes (Autenrieth 1986, Hupp and Braun 1989b). In years with heavier snow cover, most feeding activity occurs in drainages, or on south or west facing slopes (Hupp and Braun 1989b).

Availability of preferred food plants is also a factor determining winter habitat requirements (Hupp and Braun 1989b). Edelmann, et al. (1998) reviewed the literature and summarized plant characteristics for optimal wintering habitat as: 20-50% sagebrush canopy cover, 40-60 cm sagebrush height, and 0-4.5% slope. The probability of juvenile survival drops sharply outside these optima (Edelmann, et al. 1998, Fig. 5).

Inadequate winter habitat cover or winter food will reduce lipid reserves in male sage grouse (Hupp and Braun 1989a). Mating displays by males (Vehrencamp, et al. 1989), as well as egg formation and nesting activities by females are energetically demanding activities. The instantaneous energetic costs of male display (13.9 to 17.4 times basal metabolic rate) are as expensive as is flight (Rayner 1982), and thus lie at the upper extreme of the energy output that birds are capable of (sometimes termed metabolic scope) (Webb 1990). In fact, display costs are so high that they sometimes conflict with thermoregulatory expenditures (Bradbury, et al. 1989b).

Thus, breeding activities could be affected by winter habitat degradation, even if the reduction in lipid reserves was too small to affect individual survival. Because of the lekking habit and extreme degree of mate selection, this could have potent consequences for extinction risk of affected populations. Because the timing of lipid reserves, and not merely their size, is believed to be under strong selection, temporary disruption to winter foraging could affect populations, even if those lipid reserves were normal at other times (Hupp and Braun 1989a; King 1972).

Loss or reduced availability of winter habitat can have disproportionately large impacts on sage grouse over large areas because it can directly reduce population size in the next breeding season (Sands, et al. 2000, p. 27). Area effects can be especially important in winter, where episodic temporal events, seasonal events and spatial limitations combine. Hupp and Braun (1989b) reported that during the severe winter of 1984, only 7% of the 1,600 km^2 of sagebrush vegetation was available to sage grouse, primarily located in drainages. This reduction in foraging area significantly affected reproductive condition (Hupp and Braun 1989b). Unfortunately, much sagebrush removal effort is concentrated in these same drainages (Hupp and Braun 1989b). Such sagebrush removal can easily endanger the bird, even though no effects would be seen in normal winters. Beside the total amount of area available to wintering birds, fragmentation of winter habitat can cause wind penetration into those fragments (Geiger 1965), and would be an especially severe problem for wintering birds by causing hypothermia or forcing them to raise their metabolic rate for thermogenesis (Sherfy and Pekins 1995). Sage grouse are not often seen in degraded areas of winter habitat, indicating that the birds avoid such areas (Beck 1977).

The combination of such episodic temporal events, together with seasonal events and spatial limitations must be considered in determining the degree of extinction risk for sage grouse populations – a severe winter, combined with restricted or degraded foraging areas could

cause sage grouse populations to go extinct so rapidly that they would appear to evaporate from the landscape.

Lek Habitat

Open areas such as swales, irrigated fields, meadows, burns, and roadsides and barren areas or areas with low, sparse sagebrush cover are used as leks (Klebenow 1972; Ellis, et al. 1989; Klott and Lindzey 1989). Visibility on the lek itself is important for observation of male display, and visibility surrounding the lek is important for predator evasion (Gill 1965a, 1965b; Wiley 1973a). Sage grouse have tremendous site fidelity to lekking grounds and have been reported to use gravel pits, bare openings in sagebrush, wheat stubble, salt licks, remote air strips, bare exposed ridges, paved roads, knolls, dry lake beds, and the airport runways at Riverton and Jackson, Wyoming as leks (Connelly, et al. 1981; Welch, et al. 1990; Patterson 1952c, p. 280). Connelly aphorized the extreme lek fidelity of sage grouse by noting that some leks "have been used since God was a child" and J. R. Young noted that males continued to use a lek site even after a reservoir flooded the area – strutting on the bare ice, even though they were dangerously exposed to predators (Weidensaul 2001).

Of 45 leks, Patterson (1952c) reported that 11 were on windswept ridges or exposed knolls, 10 were in flat sagebrush, 7 were in bare openings, and the remaining 17 were on various other site types. In the Gunnison Basin, leks were located near river valleys Hupp (1987b, p. 56). Leks are often located near water, although water is not necessary on the lek (Call 1979). Leks are usually located on flat or gently sloping sites (Eberhardt and Hoffmann 1991, Cadwell, et al. 1994).

Leks are usually surrounded by areas with 20 to 50 percent sagebrush cover, with sagebrush no more than 1 foot (30 cm) tall (Klebenow 1972; Ellis, et al. 1989; Klott and Lindzey 1989). Nearby sagebrush for escape cover is of particular importance for leks (Welch, draft manuscript, Ch. II, p. 12). If forced to do so, sage grouse will use lek areas that lack surrounding cover – in Washington, numerous active leks exist that do not have surrounding escape cover (Tirhi 1995 citing Schroeder, personal communication). Apparently, no comparisons of losses to predators on such leks have been made to leks with predator escape cover. Some known leks have become inactive, apparently because of the lack of nearby sagebrush habitat (SMBCP 1998, p. 4). Sage grouse need relatively tall (> 12") sagebrush near the leks (within 200 m) for cover. Such nearby shrub areas are used by males for foraging, shelter, and loafing and are usually within 1 km of the lek (Rothenmaier 1979, Emmons and Braun 1984, Autenrieth 1981). Areas near the lek with good forb and grass cover, shrub heights from 18 to 38 cm tall, and canopy cover of 20% to 50% are selected by males (Call and Maser 1985, Rothenmaier 1979).

When not on the lek, sage grouse disperse to the surrounding areas (Wallestad 1975a). Some females may travel between leks. In Mono County, California, the home range of marked females during 1 month of the breeding season was 750 to 875 acres (303 to 354 ha), enough area to include several active leks (Bradbury, et al. 1989a). Gibson and Bradbury (1986) noted that prior to nesting, females may range over areas 1,000 hectares per month. Schroeder, et al. (1999a, p. 4) note that there is "no evidence that lek habitat is limiting." Such conclusions are not new. Roberson (1986) reviewed habitat relations and found that nesting, brooding, and male-feeding and loafing habitats, as well as their spatial arrangement, were more important than lek habitat. Yet, BLM and other land management agencies put great emphasis on lek area

management, "improvement," and creation (see "Management on Bureau of Land Management (BLM) Lands" section, below). If these analyses are true, then these management actions are unwarranted and a waste of agency resources. Instead, both males and females may require vast areas for foraging during the lekking time period in order to forage and store energy and nutrients.

Nesting Habitat

Sage grouse prefer relatively tall sagebrush with an open canopy for nesting. In Utah, 33 percent of 161 nests were under silver sagebrush (*Artemisia cana*) that was 14 to 25 inches (36-63.5 cm) tall, while big sagebrush of the same height accounted for 24 percent of nests (Rasmussen, et al. 1938). Sagebrush plants are preferred for nesting, and nests placed under sagebrush plants are more successful than nest placed under other bushes (Connelly, et al. 1991a, 1991b). In a three-tip sagebrush (*A. tripartata*) habitat averaging 8 inches (20 cm) in height, hens selected the tallest plants for nesting cover. No nests occurred where three-tip sagebrush cover exceeded 35 percent. Similarly, Patterson (1952c) reported that in Wyoming, 92% of sage grouse nests in Wyoming big sagebrush were in areas where vegetation was 10 to 20 inches (25-51 cm) tall and cover did not exceed 50 percent. In Idaho no hens nested in areas with less than 10 percent sagebrush cover or where sagebrush cover was greater than 25 percent (Klebenow 1972). Nest success at nest sites without sagebrush was less than half that of nests located under sagebrush (Connelly, et al. 1993). Hens also select nest sites with taller grass cover – over 18 cm in height (Connelly, et al. 1991a, 1991b; Gregg, et al. 1994). Nest predation is much greater at nests that lack grass cover, and this difference is highly significant statistically (Crawford and Delong 1993).

Klebenow (1982) found that sage grouse inhabited meadow sites with effective cover heights ranging from 7-16 cm, dependant on what was available. Dense grassy meadows that were grazed lightly or moderately were attractive to sage grouse. They avoided heavily grazed meadows in poor condition, with few grasses or forbs and dense, shrubby vegetation (Klebenow 1982). In areas where both three-tip sagebrush and big sagebrush were available, nests were typically associated with three-tip sagebrush (Klebenow 1969).

The quality of nesting habitat surrounding the lek is the single most important factor in population success (Autenrieth 1986). Where a 35% sagebrush canopy and 60 cm height are combined with residual herbaceous cover, the probability of predation is significantly reduced. As Crawford noted, herbaceous cover should be residual (i.e. left over from the previous growing season) because sage grouse initiate nests before the growing season for most grasses and forbs (Heath, et al. 1996a, p. 3, citing Crawford during discussion). The percentage of successfully nesting hens and the juvenile to adult females ratios are significantly higher in areas with robust shrub-grass production and where forbs are a common component of the spring range (Autenrieth 1986). Wallestad and Pyrah (1974, p. 632) found that successful nest had significantly greater sagebrush cover within 24 inches (60 cm) of the nest than did unsuccessful nests.

Both dense sagebrush and a healthy understory of grass cover are important components of nest habitat: shrub cover provides shading from the hot rays of the sun at midday and obscures the view of aerial, visually hunting predators such as corvids and raptors (Webb 1993b), while grass cover prevents wind penetration into the nest environment (Webb 1993b) during cold

periods and obscures the view of visually hunting ground predators such as fox and coyotes (Webb 1993b; Tirhi 1995 citing Schroeder, personal communication). The sensory ecology of olfaction is poorly understood, but grass cover probably reduces the amount of odors from the nest that waft downwind, retaining them in the boundary layer.

The amount of grass cover surrounding a nest and the height of that cover (more than 18 cm) are crucial in determining predation rates (Crawford, et al. 1992). On Hart Mountain National Antelope Refuge, Crawford and Delong (1993) found nest depredation rates of 73%, and nesting success rates of only 20%. Several studies show that shrub height and grass cover surrounding the nest significantly reduce predation. Crawford and Delong (1993) found that nests placed in grass taller than 15 cm and shrubs ranging in height from 40 to 80 cm had the lowest predation rates, and Gregg, et al. (1994) confirmed these results in an independent study, finding that greater grass canopy cover (18% vs. 5%) and greater shrub cover (41% vs. 29%) were correlated with lower nest depredation rates. DeLong, et al. (1995) obtained the same result using artificial nests. For the Western subspecies in Washington, Cadwell, et al. (1997); Sveum, et al. (1998a) and Sveum, et al. (1998b) found greater nest success on the YTC where grass and shrub cover was higher. Lower nest success was directly linked to nest predation (Sveum, et al. 1998b). Western subspecies females in Washington nested in areas with medium to very high sagebrush canopy cover (20%) and grass canopy cover (51%) (Schroeder 1994b, Sveum, et al. 1998b). It is clear that reductions in shrub cover by plowing, fire, grazing, or spraying cause reduced nest success (summarized by Schroeder, et al. 1999a). Grazing by domestic livestock is the primary land management practice affecting grass cover and height (Rickard, et al. 1975).

Even after complete cessation of grazing, grass and forb cover may not increase for years. Crawford and Delong (1993) attributed the lack of response of grass cover following cessation of grazing to the lag time in the response of vegetation to removal of grazing livestock, drought conditions, and possible competition from shrubs in limiting the establishment of new herbaceous seedlings.

Edelmann, et al. (1998) reviewed the literature and summarized plant characteristics for optimal nesting habitat as: 25-35% sagebrush canopy cover, 40-50 cm sagebrush height, 25-35% residual herbaceous cover, and 0-5% slope. The probability of a successful nest drops sharply outside these optima (Edelmann, et al. 1998, Fig. 3).

The amount and distribution of nesting habitat appears to be a limiting factor for sage grouse in the Gunnison Basin (GBCP 1997, p. 39). Nest sites in the Gunnison Basin are in taller (> 20 inches), more dense (> 25% canopy cover) areas of sagebrush than average, and have an abundance of forbs and grasses (GBCP 1997, p. 3). Residual forbs and grasses remaining from the previous season are important because females nest in mid to late April, before most herbaceous plants in the Gunnison Basin begin growing (GBCP 1997, p. 3). Sage grouse are particularly susceptible to loss of nesting habitat because they show very strong nest site fidelity (Fischer, et al. 1993a, 1993b). In recapture studies, the mean distance between nests in different years was only 550m to 680m (Berry and Eng 1985, Lyon 2000, p. 21). This is remarkable, when one considers that hundreds or thousands of square miles are available as nesting habitat.

Unfortunately, land managers often desire conditions that are directly at odds with successful sage grouse nesting. Phillips (1972) expressed a desire for sagebrush cover of 12% to 15%, but sage grouse require sagebrush cover of 20% to 50% for nesting (see below; also Welch, draft manuscript, ch. II, and Braun, et al. 1977).

Aspect and Slope

Musil (1989) found that sage grouse chose sites for nesting that had flatter slopes rather than nearby sites.

Nesting Distance from Lek

Hens often nest near the lekking grounds (Schlatterer 1960), but some hens have been noted to fly as far as 12 to 20 miles (19-32 km) to favorable nesting sites (Gill 1966a, 1966b; Rogers 1964). Wallestad and Pyrah (1974) reported that the hens traveled on average, 1.5 to 1.7 miles from the strutting grounds to their chosen nesting site. Wallestad and Pyrah (1974) found that 68% of all nests occurred within 1.5 mile of the lek (mean = 1.5 mi for adults, 1.7 mi for yearlings). Only one nest was within 1 km of the lek. Most hens moved into a relatively small area and stayed fairly sedentary until nesting. In Colorado, females regularly moved 3 to 4 miles from a lek to nest, and were observed to move as much as 7 miles away (Johnsgard 1973, p. 165, citing T. May, 1970). In some cases, nests are placed over 20 km from a lek (Schroeder 2000b). The percentage of nests that are within 3 km of a nest varies dramatically, and is often low: estimates range from 91% (Wakkinen 1990) to 55% (Autenrieth 1981), down to 20% (Hanf, et al. 1994) and as low as 15% (Schroeder, et al. 1999a, p. 17). Estimates of nests within an annulus of any given size may be methodically inflated, as the closest areas to a lek are smaller and easier to search thoroughly than are the larger areas at increasing radii from a lek. Habitat guidelines that protect only a few km within a lek site are inadequate, and this has been known for years (Wakkinen, et al. 1992b).

In general, it will not be possible to adequately protect sage grouse nesting habitat by simply restoring habitat within a 2-3 mile radius of a lek site; instead, habitat within 20-30 miles of a lek site must be restored – and perhaps more, as radio telemetry studies cannot yet locate birds at great distances from the receiver. Oddly, a number of Environmental Impact Statements (EISs) and Environmental Assessments (EAs), have analyzed impacts on sage grouse solely in terms of nesting and lekking habitat. This is completely inappropriate. Sage grouse need habitat to carry out all of their life-history stages.

Nesting Distance to Other Habitat Components

Autenrieth (1986) found no relationship to proximity of water, meadows, or a brood food source such as anthills.

Feeding and Roosting Habitat in the Nesting Season

During the nesting season, cocks and hens without nests use relatively open areas for feeding, and roost in dense patches of sagebrush (Klebenow 1969, 1972).

Edge Effects

Musil (1989) found that sage grouse selected nest sites farther from habitat edges, with more litter cover, less bare ground, and a greater density of mountain big sagebrush than in nearby areas. The probability that a site would be used as a nest site increased as the distance from habitat edge and the density of mountain big sagebrush increased.

Creation of edge greatly increases predation. Construction of linear facilities (such as pipelines, fences, roads, and powerlines) and the concomitant clearing of long swaths of land, is a major generator of edge habitats, which are favored by many predators on sage grouse.

Brooding Habitat

Brooding habitat requires relatively open canopy cover and abundant insect prey and forbs in close proximity to denser sagebrush stands for predator escape (Schroeder, et al. 1999a; Braun, undated, b). Brooding sites contain twice the forb cover as surrounding areas (APA 1998, p. 129). Juvenile sage grouse stay mostly in open sagebrush with a forb component through June (Gill 1965a, 1965b; Savage 1969a). As the season progresses, they move to riparian areas and other areas still containing green vegetation, such as meadows and areas associated with permanent and intermittent streams, springs, and seeps. By August, they are often clustered near permanently wet meadows and other such sites (Gill 1965a, 1965b; Savage 1969a, Klebenow 1969). Such riparian areas are of particular importance in dry years, as they may be the only food source for chicks (Miller and Eddleman 2000). Many such riparian areas have been destroyed by water developments for livestock or by conversion to agriculture. Indeed, 95% of the riparian habitats in the West have been altered, degraded, or destroyed (Ohmart 1994). Livestock grazing is the "most insidious threat to riparian habitats (Carothers 1977, p. 3, Ohmart 1994). "Riparian areas have been extensively impacted within the Columbia Plateau such that undisturbed riparian systems are rare" (Altman and Holmes 2000, p. 8; citing Knutson and Naef 1997). Other significant threats include dams, reservoirs, ground water depletion, instream flow reduction, flood control, and river flow and hydrology alteration (Ohmart 1994). BLM found that only 7% of riparian-wetland habitats were meeting management objectives (GAO 1992a). Young sage grouse are highly dependent on riparian and meadow vegetation until after 11 weeks of age (Oakleaf 1970).

High levels of food and shelter provided by forbs, grasses and low sagebrush are key requirements for chick survival (Klebenow 1972, 1985). Broods often make use of open meadows (Bean 1941, Carhart 1942, Eng 1952a, Rogers 1964, Klebenow 1969). For this reason, any effect that causes stream channelization, and reduces the belt of wet forbs and other vegetation that occur at considerable distances from streams, will harm populations at this critical stage. Livestock grazing is a notable cause of stream channelization.

In 158 Montana locations, young broods used areas of low plant height (9 to 15 inches [23-38 cm]) and density, while older broods and adults used areas where plants were taller (7 to 25 inches [18-63.5 cm]) (Martin 1970a). In areas where both three-tip sagebrush and big sagebrush were available, broods were typically associated with big sagebrush (Klebenow 1969). Moreover, birds avoided extremely dense sagebrush stands, where forbs were lacking (Klebenow 1969). Broods moved higher in elevation as the summer progressed, following a gradient of green food plants such as forbs (Klebenow 1969).

Early brood rearing habitat has a relatively open canopy of sagebrush and a fairly low height of sagebrush. Canopy cover was less than 25% in Montana (Wallestad 1975a, Martin 1976), and less than 31% in Idaho (Klebenow 1982), and these sites were primarily associated with feeding. Also in Montana, Peterson (1970b) found canopy cover to be 6% and shrub heights to range from 15 to 30 cm in June, and by August canopy cover was 12% and shrub heights ranged from 30 to 45 cm. Pyrah (1971) found canopy cover was 14% in June and increased to 21% by September. Birds in Oregon used low sagebrush for the first 6 weeks post-hatch, and moved into taller sagebrush (big sagebrush) stands as they matured (Drut 1993; Drut, et al. 1994a).

It is thus reasonable to divide the brooding season and life history stage into the early brooding season and the late brooding season. The key event marking the difference between the two is the diminished availability of forbs for the juveniles. Hens with broods generally remain in upland habitats as long as forbs remain available, then move to more mesic sites (Drut 1994). These movements emphasize the crucial importance of forbs to juvenile sage grouse. In years with greater precipitation, hens delay their movements to mesic areas because forbs remain available longer in the upland sites (Klebenow 1969, 1985; Wallestad 1975a; Autenrieth 1981; Drut 1994). Grazing or other effects that remove or damage forb cover or grass cover damage sage grouse habitat and productivity. This has already occurred over the entire range of the bird (Connelly and Braun 1997; Braun 1998a, 1999a; Paige and Ritter 1999).

Broods require forbs, insects and cover for growth, concealment and shade (Autenrieth 1986; Patterson 1952c). Where these requirements are met at or near the nest site, the brood moves less, reducing exposure to predation and conserving energy (Autenrieth 1986). Birds also use denser areas of sagebrush in late summer when the forbs on preferred habitat are desiccated (Wallestad 1970, p. 25). On dry ranges, however, broods are forced to move to the nearest meadow for attaining their needs. Broods follow moisture gradients to higher elevations (Oakleaf 1971) or move to bottom lands and fields where forbs are more available (Klebenow 1969; Peterson 1970b; Wallestad 1975a; Call and Maser 1985; Connelly, et al. 1988; Sveum, et al. 1998b). Such movements expose the young birds to predators and desiccation, and can deplete their energy reserves. When the birds move to farmed fields, they may become exposed to high levels of pesticides and herbicides, as well as enhanced predation or attacks by domestic dogs and cats. Hens remain near the nest site with their broods until forced to move by desiccation of the vegetation (Gregg, et al. 1993; Connelly, et al. 1988). In wetter years, movements away from the nesting area is delayed (Klebenow 1969, 1985; Wallestad 1975a; Autenrieth 1981). Thus, any activities that cause drying of nesting area vegetation, such as stream channelization by cattle or ground water pumping for livestock "guzzlers," will increase the threats to the birds by forcing the hen to prematurely move her young brood into or through areas with high predation risk.

Upland meadows receive concentrated use in late summer because forbs and water can only be obtained in those areas (May and Poley 1969b, Oakleaf 1971, Schoenberg 1982, Klebenow 1985, Evans 1986). Because water projects and livestock operations have concentrated the areas where forbs and water can be obtained, the birds concentrate in those areas. Unfortunately, this aggregation exposes the birds to predation and disease spread. Birds appear to select for smaller meadows over larger ones (Oakleaf 1971, Drut 1993), again illustrating that predation pressure is a significant effect away from shrub cover.

Edelmann, et al. (1998) reviewed the literature and summarized plant characteristics for optimal brooding habitat as: 15-20% sagebrush canopy cover, 30-40 cm sagebrush height, 30-40% residual herbaceous cover, and 0-5% slope. The probability of brood survival drops sharply outside these optima (Edelmann, et al. 1998, Fig. 4). The authors did not separate early and late brooding habitat in their analysis.

The importance of wet meadows to sage grouse cannot be over emphasized, and "has been repeatedly demonstrated" throughout the range of both species (GBCP 1997, p. 4). The best and most recent scientific data show that a 200 m band of sagebrush around wet meadows is

required by sage grouse (Dunn and Braun 1986b; GBCP 1997, p. 3) – the 100 m band of vegetation recommended in earlier studies is inadequate (GBCP 1997, p. 3).

Like the effects of environmental variation on winter habitat discussed above, combined effects could operate at other life history stages, in particular the highly susceptible brood-rearing stage. Episodic summer drought reduces insect populations needed by juveniles, and juvenile mortality over the summer period may be even more variable than mortality over the winter (Rich 1985a, p. 13).

Western riparian habitats are assemblages of plant communities occurring at interfaces of terrestrial and aquatic communities. They create well-defined, narrow zones of vegetation along ephemeral, intermittent, and perennial streams and rivers. "Riparian areas are among the most threatened habitats on the continent" because they are favored for many uses including livestock grazing, agriculture, water management, timber harvest, recreation, and urbanization (Saab, et al. 1995). The extent and type of riparian vegetation in the Columbia Basin has changed significantly. There has been a decline in shrublands in the riparian zones in more than half the Ecological Reporting Units (ERUs) in the Basin (Quigley and Arbelbide 1997c, p. 1086). These types of areas are the most modified in the West (Chaney, et al. 1990, 1993a). Grazing on riparian areas in arid lands is particularly damaging (Platts and Nelson 1985; Chaney, et al. 1990, 1993a; Platts 1981a-c, 1991). Livestock grazing effects riparian vegetation by altering, reducing, or removing vegetation, and by actually eliminating riparian areas through channel widening, channel aggrading, or lowering the water table (Platts 1991). The quality, amount, and distribution of early brooding habitat appears to be a limiting factor for sage grouse.

Non-brooding Birds During Summer

During summer, females without broods and males select big sagebrush stands with canopy cover ranging from 20% to 35% (Patterson 1952c, Martin 1970a, Wallestad and Schladweiler 1974, Wallestad 1975a; Braun, et al. 1977; Ellis, et al. 1989). During summer and early fall, male sage grouse remain segregated from brood and hen flocks, typically remaining within 2 to 3 miles (3.2 - 4.8 km) of the lek (Wallestad 1975a). Hens without broods and male flocks are less dependent on wet meadows and riparian areas than are hens with broods; however, some dependence is still present, and these birds follow the same habitat use patterns as do hens with broods (GBCP 1997, p. 4).

Fall Habitat

Dalke, et al. (1963) reported that birds collected near water holes as temperatures approached freezing. Birds usually remained in a single place for several days, and then moved out in groups. Pyrah (1954) reported that immature females were the first to leave for wintering areas, followed by mature females, then adult males.

Habitat Degradation

Degraded habitats typically do not support as many individuals as higher quality habitats, but may support an equal number of breeding males (Gibbs and Faaborg 1990). Thus, surveys of breeding males may overestimate population viability (Gibbs and Faaborg 1990). Mechanistically, this effect can arise when degraded or marginal habitat is adequate for males but not for breeding females, a condition that is likely common throughout sage grouse range.

Habitat loss and degradation are the "most frequent causes of species endangerment" (Schwartz 1999, p. 86; Wilcove, et al. 1993; Foin, et al. 1998).

Sagebrush habitats have been degraded by a wide variety of effects, ranging from depletion of the understory plants needed for juvenile and female nutrition, to erection of structures that serve to enhance predator populations, to outright removal of sagebrush itself. In many cases, sagebrush removal has been touted as a way to enhance wildlife populations, even including sage grouse. Sagebrush removal will not benefit sage grouse unless increased forb production occurs, and only if sagebrush density does not become too low (Autenrieth 1986). Sagebrush has been removed with herbicides, intense fire, and by chaining or bulldozing in most of the range of the sage grouse. Livestock grazing has spread exotics such as cheatgrass, removed valuable cover, and reduced forbs to such an extent that birds are apparently unable to maintain adequate nutritional levels for periods of high nutritive demand, including egg formation and development. Consequently, populations have plummeted.

Moving livestock away from riparian areas (for example, to improve fish and riparian habitat, or to improve late season brooding habitat for sage grouse) could pose a significant detriment to upland habitat that sage grouse rely on for most of their life history.

In one study, Webb (1993b) was unable to find even small portions of non-degraded habitat in Wyoming outside of a National Park. This accords with the findings of Connelly and Braun (1997), Braun (1998a, 1999a), and Paige and Ritter (1999) as well as with the findings of plant ecologists. For example, with respect to sagebrush ecosystems, West (2000, p. 16) stated "pristine ecosystems ... no longer exist, nor are they likely to be recoverable;" moreover, any areas of sagebrush that have escaped "direct human influences" exist only as "remnants" and as "relicts" that are not complete ecosystems. Only about 1% of sagebrush lands are in such relicts and about 5% has an understory dominated by native herbaceous vegetation (West 2000, Fig. 4, p. 23; Sands, et al. 2000, p. 29). About 25% of sagebrush lands have severely depleted herbaceous understories, while about 25% has an understory composed of annuals (which provides marginal nesting cover and little forage value for sage grouse), and another 25% of the landscape has already converted to annual grasslands of no value at all to sage grouse (West 2000, Fig. 4, p. 23; Sands, et al. 2000, p. 29-30). The remainder consists of crested wheatgrass, knapweeds, yellow star thistle and mixtures of these invaders (West 2000, Fig. 4, p. 23; Sands, et al. 2000, p. 30-31). Thus, only about 6% of the sagebrush landscape is of much value as habitat. The scope of habitat degradation and the various threats causing degradation are discussed throughout this review, but salient point is particularly chilling: West (1999b) estimated that 50% or more of historical sagebrush areas had reached vegetative transition states, dominated by exotic plants, from which they could not be recovered at all, given current technology (see also Wisdom, Rowland, et al. undated). These habitats are gone forever.

Habitat degradation causes severe endangerment to species. Successful recovery of species under the ESA has primarily involved species threatened with predation and pollutants. "It is much more difficult to recover species where habitat degradation and loss are the primary causes of endangerment" (Schwartz 1999, p. 86). Because this is the case with sage grouse, the Service should act promptly and comprehensively to list sage grouse and to restore habitats.

Home Range

Home range size varies with season, being smallest in summer, but is generally larger than those of other grouse (Bergerud 1988b). Summer home ranges may range from 3 to 7 km^2 (Connelly and Markhamer 1983, Gates 1983). Annual home ranges may be as large as 1,500 km^2 (577 $mile^2$) (Paige and Ritter 1999, p. 33, citing unpublished data of Connelly). On the YTC in Washington, home range sizes are 24 to 26.6 km^2 in summer and spring, and 44.2 km^2 in fall (YTC CA 1994). Home range sizes will be much larger for grouse that travel some distance among different habitat components than for those birds that have all the habitat types they need adjacent to each other. Home ranges will also be small in birds that simply cannot find their needed habitat except in a small remnant land area. Habitat degradation or fragmentation is likely to result in larger home ranges as birds must travel further and further to find needed resources.

Habitat Fragmentation and Landscape Effects

Habitat fragmentation is one mechanism that has been proposed to explain declines in a number of species, and has perhaps been most extensively studied in forest dwelling birds, particularly neotropical migrants (Wilcove, et al. 1986; Finch 1991; Faaborg, et al. 1993; Morrison, et al. 1992a; Sherry and Holmes 1993). Fragmentation effects are by no means restricted to forest landscapes, however, and have been frequently demonstrated in flat, or two-dimensional landscapes such as sagebrush shrub-steppe (Johnson and Temple 1986; Burger, et al. 1994; Herkert 1994; Knick and Rotenberry 1995b, 1999b, p. 105; Welch draft manuscript, ch. II) and specifically, in sage grouse populations (Kerley 1994; Commons, et al. 1996a; Schroeder 1994a, 1997b). Forest fragmentation effects are not qualitatively different from those in the sagebrush shrub-steppe (Wiens 1989b, II, p. 204). Moreover, sage grouse may be unusually sensitive to fragmentation effects because of their specialized food habits, generalized anti-predator strategies, and other life history factors (Braun, et al. 1994, p. 432). Both coarse-grained and fine-grained fragmentation can affect sage grouse (Braun, et al. 1994, p. 433), and sage grouse are considered to be "area-sensitive species" (Sands, et al. 2000, p. 31; Altman and Holmes 2000, p. 25). Because sage grouse have narrower habitat requirements than do sharp-tailed grouse and depend so strongly on sagebrush, their area requirements for even a small group of birds – much less a viable population – will greatly exceed the estimate of 3,000 hectares for sharp-tailed grouse (Sands, et al. 2000, p. 31).

Habitat fragmentation occurs when a large tract of habitat is dissected into smaller patches isolated by other habitats or vegetation types different from the original (Wilcove, et al. 1986; Morrison, et al. 1992a; Faaborg, et al. 1993). These patches (also referred to as fragments, islands, or isolates) are redistributed into variable sizes, shapes, and locations from the original area (Diamond 1975a; Wilcove, et al. 1986; Morrison, et al. 1992a; Faaborg, et al. 1993). Fragmentation causes increased extinction risk and population declines as compared to habitat loss alone (Andren 1994). When fragmentation effects exist, species abundance is less than that expected from the total amount of habit present; instead, abundance is more closely related to a smaller metric – the area of patch interior present, termed "core areas" (Temple 1986a). Forman and Godron (1981) offer a readable introduction to patch dynamics, and a variety of textbooks offer simple introductions to fragmentation concepts (Primack 1993, Meffe and Carroll 1997). Wilcove (1987) identified four ways that fragmentation can cause extinction: (1) a species can be