A Comprehensive Rapid-assessment Approach for Research Agenda Development: Elk (*Cervus elaphus*) at Yellowstone National Park

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ABSTRACT

In 1992, the National Research Council (NRC) summarized the broadest purposes for research in national parks as 1) to determine what resources are present in order to protect, manage, and detect changes in them; 2) to understand the natural dynamics and processes of populations, ecosystems, and other park resources; and 3) to assess the effects of specific threats and to devise and evaluate management responses. In order to successfully act upon these recommendations, individual parks must move into the realm of local science planning and implementation. We developed a systematic, rapid assessment approach that incorporated conceptual models and a critical review of published literature to identify knowledge gaps regarding elk ecology on Yellowstone National Park's (YNP) northern range. Additionally, to demonstrate the potential utility of integrating our understanding of existing knowledge gaps with management issues, we developed an "urgency" index that addressed issues of temporal dynamics and issues of management concern in YNP. Our findings revealed that with respect to elk in YNP, relations with parent material and beaver have yet to be scientifically addressed, while geothermal features/events and topographic influences have been inadequately researched in comparison to other system components. In contrast, elk relations with grassland and fire have been relatively well studied in the YNP. After accounting for management urgency, our model indicated those elk-centric topics concerning disease, predation, beaver, humans, and competition should receive the highest research priority, and those involving elk relations with grasslands, coniferous forest, topography, and aspen should receive the least. Our process provided a series of logical steps for organizing research results via a system perspective, and a way of linking science with management. We encourage other parks to utilize this method to develop robust conceptual frameworks that underpin long-lived and integrated systems-oriented science programs to better understand and manage park resources.

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One should not be too ready to embrace a conjecture that comes into the mind; it must be submitted to most careful scrutiny before being accepted even as a tentative hypothesis, for the main danger lies in the idea that seems so "obvious" that it is accepted almost without question.

Beveridge 1950

The National Park Service must engage in a sustained and integrated program of natural, cultural and social science and research aimed at acquiring and using the information needed to manage and protect park resources.

The Vail Agenda 1992

The fact is, we don't and cannot know how abundant white-tailed deer were in Gettysburg National Historic Park or elk or bison were in Yellowstone NP in prehistoric times. By definition, they are prehistoric. So all we can do is guess, however educated that guess might be.

McNaughton - 1995

INTRODUCTION

The National Park Service entered a new era of scientific accountability with the passage of the National Park Omnibus Act in 1998, specifically Section 202, wherein "*The Secretary (of Interior) is authorized and directed to assure that management of units of the National Park System is enhanced by the availability and utilization of a broad program of the highest quality science and information.*" The importance and roles of research in the national parks has been oft discussed with seeming repetition, but generally decrying the overall lack of strategic science agendas with clear linkages to both pressing park management issues and identification of long-term ecosystem structure and function (Leopold 1963, Allen and Leopold 1977, Castleberry 1987, NPCA 1988, NRC 1992, NPS 1992, Keiter and Boyce 1991, Wright 1992, Pritchard 1999). The National Research Council (1992) recommended that research in the national parks should 1) determine what resources are present in order to protect them, manage them, and detect changes in them, 2) understand the natural dynamics and processes of populations, ecosystems, and other park resources, and 3) assess the effects of specific threats and to devise and evaluate management responses. Yet, in order to successfully extend beyond such predictably thematic recommendations, individual parks need to facilitate deliberative local science planning and implementation. The question remains how individual parks and park networks can develop integrated long-lived science programs to achieve these broad objectives. We believe that the National Research Council (1992:92) provided a most appropriate recommendation: "*The NPS should support and develop intensive long-term, ecosystem-level research patterned after the National Science Foundation's (NSF) Long-Term Ecological Research (LTER) program.*"

We do not interpret this recommendation to mean that each park needs or could become a functional LTER program under the auspices of the NSF. Rather we consider the NRC

(1992) recommendation as a charge to the national parks to adopt the science planning, implementation, analysis and synthesis processes inherent to LTERs. The LTER program is built upon a foundation of multidisciplinary and collaborative investigations of whole ecosystems and their component organisms and processes to identify and understand general ecological phenomena across longer temporal and spatial scales; create a legacy of long-term experiments and observations that are soundly designed and adequately documented for the use of future generations of scientists; advance ecological science by conducting major synthetic and theoretical efforts; and provide information for identifying and solving societal (e.g., park stewardship) problems. Fundamental to any of the 24 LTER research programs located across the United States is a conceptual framework that describes the state-of-the-art understanding of the linkages and relationships between ecosystem drivers, stressors, effects, ecological and sociological outcomes, and measurable parameters.

Too often, critical information gaps become apparent when a divisive park resource issue emerges through crises that pit one or more park constituencies against another, with inherent divisiveness inflamed by adherence to poorly documented or blatantly unreliable knowledge. National parks and their legislative and judicial constituencies often react to conflicts by recommending expensive expert committees or panels to review, analyze and synthesize the existing information and make recommendations about the state of the park's ecosystems and research needs (NRC 1998). Although these scenarios are periodically necessary, it does not have to be the norm. Indeed, we believe that parks inherently possess the proactive capacity to critically and deliberately self-address information gaps and needs. Further, we believe that this capacity building does not have to come with an extensive timeline or a burdensome budget.

We recommend that the basic foundations of successful long-term research in national parks are transparent and deliberate science agendas that offer the substructure for the interest, creativity and productivity of individual scientists, working alone and together, and finding creative ways to support both site-initiated research and networked-research. Herein, we propose a comprehensive rapid assessment approach for the development of long-term park-based science agendas and utilize an elk-centric case study.

General Conceptual Framework. The development of conceptual models of park ecosystems involves the identification, inclusion, and scale-dependent linking of system variables such as drivers, stressors, effects, attributes, metrics (NPS 2003); state variables, constants, auxiliary variables, material transfers, sources and sinks (Grant et al. 1997), and other variables, often in a hierarchal form (Gentile 2001). It has been suggested that the inclusion of variables into conceptual models can take two forms (Jorgensen 1988, Grant et al. 1997). The first involves inclusion of a limited suite of variables that are as reductionist as practicable and subsequent additions of critical components that were initially overlooked. The other approach is to include at the onset virtually all model components that could possibly have any importance and then delete the superfluous ones (Grant et al. 1997). Given the inherent levels of uncertainty in ecosystem modeling, it is often better to use a slightly more complex model over a simplistic. The criteria used for inclusion or exclusion of conceptual ecosystem model

variables, thus determines the pool of variables that is drawn upon for the selection of ecological indicators that possess the desirable characteristics described below. Indeed, the desirable characteristics of conceptual model variables must then underpin those of ecological indicators. Grant et al. (1997) suggests that conceptual model variables and components have the following desirable characteristics: 1) *state variables* should represent vertices of accumulation of resources within an ecosystem (e.g., energy contained in plants, herbivores, predators); 2) *driving variables* should affect but not be affected by the rest of the system (e.g., transfer of energy from the sun to plants and associated seasonal patterns); 3) *constants* should not vary under assumptions of the conceptual model (e.g., coefficients that are part of a rate equation); 4) *auxiliary variables* arise out of calculation and should represent explicit model concepts; 5) *source and sink variables* represent origin and termination points of material transfers (e.g. energy) into and out of a system; 6) *material transfers* should describe quantitatively the flow of material (e.g. nutrients) between two state variables, between a source and a state variable, or between a state variable and a sink.

Fancy (2003) recently described a suite of top-to-bottom hierarchal conceptual model components including: *drivers/disturbances* that are major large-scale influences on natural systems; *stressor/consequences* that cause significant changes in ecological components, patterns and relationships in natural systems; *ecological effects* that are responses to drivers and stressors; *attributes/indicators* that are any information rich living or non-living feature of an ecosystem that may be independent or integrative and can be measured or estimated and that provide insights into the state of the ecosystem; *measurements* of specific measures of an attribute or indicator.

Yellowstone Herbivore Conceptual Framework. East Africa's seasonal migrations of large ungulates and their suite of predator and scavenger dependents is among the world's most spectacular natural phenomena. Rooted in eons of evolution, this expansive spatial and temporal process demands huge landscapes that dwarf the confines of any single preserve. A long-term program of multi-disciplinary and integrative science has been envisioned and underway in the Serengeti of East Africa for over 40 years (Sinclair and Norton-Griffiths 1979, Sinclair and Arcese 1995). Because of its relatively high diversity and abundance of ungulates, as well as similar patterns of primary productivity, Yellowstone National Park has been referred to as the Serengeti of North America (Berger 1991, Frank and McNaughton 1992, McNaughton 1996, Frank et al. 1998). Yellowstone's eight ungulate species conform to a variety of behavioral, size, and habitat templates. Some, like white-tailed deer (*Odocoileus virginianus*) and mountain goat (*Oreamnos americanus*) are uncommon or historically absent from the park (Yellowstone National Park 1997). Others, such as elk (*Cervus elaphus*) and bison (*Bison bison*) are numerically dominant, and highly visible. These two species combined account for 88% of the total number of individual ungulates (Table 1) and 95% of the ungulate biomass (standing crop)(Table 2) in Yellowstone's northern range, and they are key components of ecosystem function (Frank and McNaughton 1992, Hobbs 1996, Dieni et al. 2000) and recreation (Delgiudice et al. 1991, Schullery 1997, Huff and Varley 1999). These species are also controversial – in part because of their abundance and equivocal historical records (Chadde and Kay 1991, Kay 1994, Yochim 2001), but also because their seasonal

travels outside of the park create management challenges that are perceived differently by a diverse public including citizen organizations, and government agencies.

Numerical abundance is not a prerequisite to Yellowstone ungulate controversy or recognized importance (interestingly, rodent populations can alter the appearance and function of Yellowstone grasslands [Gruell 1973, Meagher 1973], and may be the primary prey for carnivores in terms of numbers and biomass [Johnson and Crabtree 1999]). Clearly, rodents and other small mammals outnumber all other vertebrates in Yellowstone's northern range. When compared to ungulates, rodents (excluding beaver and porcupine) combine to account for at least 20% of total mammal herbivore biomass (Table 3), and their addition to the measure of community diversity elevates H' and J' nearly twofold (Tables 2 and 3). Their role in ecosystem and landscape processes in an animal community noted for its large mammal diversity may outweigh most of Yellowstone's more visible ungulates (the addition of lagomorphs and the previously mentioned larger rodents would clarify future analyses of mammal community structure and function). Nonetheless, relatively uncommon ungulates such as moose (*Alces alces*), pronghorn (*Antilocapra americana*) and bighorn (*Ovis canadensis*) are important management concerns due to the selective browsing and successional changes that may be caused by the former, and the precarious population status of the latter two. Whereas the Greater Yellowstone Ecosystem is peripheral to the North American distribution of several of its ungulate species, it is the distributional center for others. This is an important consideration for managers inasmuch as a species at the limits of its range is expected to exhibit demographic fluctuations that may lead to occasional local extinctions that are caused by climatic, competitive, predatory, or anthrpogenic influences among others (Kyle and Strobeck 2002). Such is not the case for elk and bison in Yellowstone. The park and its environs are central to these species' historical North American ranges, but Yellowstone was an important refugium that facilitated the recovery of both species following the 19th century period of human-induced range-wide decline (Houston 1982, Huff and Varley 1999).

Yellowstone Elk Conceptual Framework. We propose a non-equilibrium elk-centric conceptual framework as a logical consequence of the defining characteristics of the Yellowstone Northern Range, which are products of multiple limiting factors and complex interactions. McNaughton (1983) stated, "Undue emphasis on competition or predation or disturbance or any other single, composite factor as a community organizer is highly misleading in the context of Serengeti grasslands, and I believe, communities in general." As in the Serengeti, grasslands of North America, including the montane communities of Yellowstone's Northern Range, are characterized by multiple influences in space and time, wherein biotic interactions such as herbivory, competition, and predation can be influenced as strongly by each other as by abiotic factors (Collins et al. 1998).

Because of its abundance, wide-ranging movements, economic value, and social status as both a conservation flagship and potential economic liability, the elk of Yellowstone's northern range is a logical framework for the development of long-range research planning that seeks to clarify "plant and soil responses to climate and herbivory, as well

as natural interactions between plants, herbivores, and predators over both short and long time scales" (Coughenour and Singer 1991:210). This need is made even more urgent as reintroduced wolves (*Canis lupus*)(Yellowstone National Park 1997, Fritts et al. 2001, Smith et al. 2003) establish a widespread and growing presence in the Greater Yellowstone ecosystem. Wolf predation on elk, coyote, and other species has the potential to rearrange interspecies relations and renew others that have not operated in the Yellowstone area for more than 70 years (Smith et al. 1999, Smith et al. 2003). Some estimates project reductions of up to 30% for the northern range elk herd as a result of wolf predation (Boyce and Gaillard 1992, Mack and Singer 1992, Boyce 1995).

For Yellowstone National Park to move closer to its mandate of "natural process management" (see Huff and Varley 1999), it will need to better understand the ecosystem processes that operate at the landscape scale including hydrology, fire, predation, herbivory, disease, and animal migration. Well-planned research will be needed to provide quantitative documentation and predictions of dynamic system responses to forcing functions characterized by legacies, time lags, complex interactions (e.g., large mammal interrelations, plant succession, and landscape processes as the vertebrate and plant communities respond to changes in climate, hydrology, animal species diversity and abundance), and management contingencies (Collins et al. 1998). Again, as noted by McNaughton (1983), these contingencies are not capricious but probabilistic. Yellowstone National Park will optimally benefit from deliberate multi-disciplinary and integrative research planning and implementation only when information and insights gain form through synthesis, a reliable foundation for a more thorough understanding of North America's most complex predator-prey system, that will in turn enable the National Park Service to better engage the complexities of natural process management within a matrix of emerging social deterrents.

We utilized a systematic approach that incorporated conceptual models and a critical review of published literature to identify gaps in research regarding elk ecology on Yellowstone National Park's northern range. The primary goal of our effort was to create a mechanistic tool to help managers convert and organize large amounts of information on a given topic into effectively identified, prioritized, and planned research and management of natural resources. This process is intended to identify future research needs to both increase the understanding of elk ecology on the northern range and meet management objectives. For our tool to have maximum utility, we constrained its framework to:

1) Provide a series of logical steps for organizing research results via a system perspective;
2) Incorporate filters that index the inferential power of published literature and, thus, the degree of reliable knowledge provided;
3) Serve as a way for scientists and managers to achieve a consensus regarding the primary resource-related issues, research gaps, and potential scientific avenues for resolving these issues; and
4) Provide a way of linking science with management.

Table 1. Estimated population sizes (Singer 1991, Yellowstone National Park 1997), diversity (H') and evenness (J') (Shannon and Weaver 1949) of six ungulate species with populations ≥200 in the northern range of Yellowstone National Park.

Species	Population size	Proportion of total	H'/J'
Elk	17,400	0.84	
Bison	900	0.04	
Mule deer	1,700	0.08	
Pronghorn	300	0.014	
Moose	200	0.009	
Bighorn	180	0.009	
Total	20,500		0.61/0.34

Table 2. Estimated biomass (standing crop) based on mean adult female mass (Houston 1982), diversity (H') and evenness (J') (Shannon and Weaver 1949) of six ungulate species with populations ≥200 in the northern range of Yellowstone National Park.

Species	Population size	Adult female mass (kg)	Species biomass (kg)	Proportion of total biomass	H'/J'
Elk	17,400	240	4,176,000	0.87	
Bison	900	450	405,000	0.08	
Mule deer	1,700	60	102,000	0.02	
Pronghorn	300	50	15,000	0.003	
Moose	200	300	60,000	0.01	
Bighorn	180	60	12,000	0.002	
Total	20,500		4,770,000		0.48/0.27

Table 3. Estimated biomass (standing crop) based on mean adult female mass (Houston 1982), diversity (H') and evenness (J') (Shannon and Weaver 1949) of six ungulate species with populations ≥200 and rodents (excluding beaver and porcupine) in the northern range of Yellowstone National Park. Rodent biomass was extrapolated from data presented by Crabtree et al. (1997) and Sirotnak and Huntly (2000), and likely is a significant underestimate of actual rodent abundance in the system.

Species	Population size	Adult female mass (kg)	Species biomass (kg)	Proportion of total biomass	H'/J'
Elk	17,400	240	4,176,000	0.71	
Rodents[1]	15,769,200	0.08	1,063,860	0.18	
Bison	900	450	405,000	0.07	
Mule deer	1,700	60	102,000	0.017	
Pronghorn	300	50	15,000	0.002	
Moose	200	300	60,000	0.01	
Bighorn	180	60	12,000	0.002	
Total	15,789,880		5,833,860		0.88/0.46

[1] A single pocket gopher (*Thomomys* spp.) is capable of moving 1,130 kg of soil/year (Richens 1966).

METHODOLOGY

Step 1: Preliminary Review. We identified the interactions and relationships that best explain how elk affect and are affected by other components and processes of the northern range. This also allowed us to become familiar with elk-related issues and controversies that routinely affect the park. We did this over a two-week period through informal meetings with various park biologists, and by reviewing historical documents, internal reports, and publications. Additionally, we went into the field by ourselves and with biologists that were currently working on research projects in the park. These excursions allowed us to become familiar with YNP's landscape, wildlife, current research, and sociological phenomena. Throughout the preliminary review period the project's 6-person team met on several occasions to brainstorm in an attempt to better understand and identify potential causal hypotheses that explained the ecology of the northern range. The final product of the initial review was an eight-page summary of the existing management and research situation on Yellowstone's northern range.

Step 2: Conceptual Model. Following our preliminary review, we constructed a non-quantitative conceptual model that identified the relationships between elk and other system components and processes. This model was essential for effectively identifying the major ecological and anthropogenic factors that influence the northern range ecosystem. Our conceptual model followed a top-down hierarchy with these components: 1) drivers: forces that have large-scale influences on the system (these can be natural e.g., climate and topography or anthropogenic); 2) primary stressors: the physical or chemical changes that occur within natural systems that are brought about by the drivers, and which cause significant changes in the biological components, patterns, and relationships in the system. 3) secondary stressors: the physical or chemical changes that occur within natural systems that are brought about by the drivers and primary stressors, and which can cause significant changes in the biological components, patterns, and relationships in the system; and 4) ecological effects: The biological elements of interest (e.g., elk population ecology and etc.) (Gentile et al. 2001). After constructing the conceptual model, it was reviewed independently by several people with extensive experience with northern range ecology to ensure conceptual accuracy. The revised conceptual model was then used to identify pathways of ecological interactions, or hypothesis frameworks.

Step 3: Literature Review. We conducted an exhaustive literature review that focused on Yellowstone's northern range elk population. We used the literary archives at Yellowstone National Park, a computerized search of the University of Kentucky (Infocat) and Montana State University libraries, and an online search of the databases, *Biological Abstracts* and *Wildlife and Ecology Studies Worldwide*. Citations were placed in a bibliography categorized into the ecological variables and interactions generated in the conceptual model.

Step 4: Literature Evaluation and Annotated Bibliography. We categorized the literature in the bibliography according to each inferential power (IP). Each paper was reviewed and assigned to one of seven IP categories.

1) Mechanistic explanation of phenomenon, process, or relation with an inference ($P<0.05$) based on an experimental approach (e.g., controls vs. treatments).
2) Mechanistic explanation of phenomenon, process, or relation with an inference ($P<0.05$) based on a descriptive/observational approach using an *a priori* sampling design.
3) Conclusions based on a descriptive approach with an *a priori* sampling design ($P<0.05$) but without a mechanistic explanation.
4) A data-based treatment without statistical/inferential power that proposes a mechanistic explanation (includes predictive projections based on previously published works that provide mechanistic explanations or objectively derived natural history (categories 1, 2, & 5).
5) A synthetic overview of existing literature or theory that offers a conceptual framework within which to examine temporal or spatial phenomena.
6) Observational or anecdotal natural history without sampling design that is opportunistic or retrospective in nature.
7) Reference to another publication is made, but no elaboration is offered (the paper is removed from further consideration)

We annotated each paper and recorded the following information: 1) paper topic(s); 2) publication outlet (book, journal, or gray literature); 3) IP category; 4) statement of purpose; 5) summary/conclusions; and 6) stated hypotheses (both tested and suggested) and whether tested hypotheses were supported or rejected.

Step 5: Reconciliation of Reviewed Literature and Hypothesis Frameworks. The hypotheses identified from the published literature were placed within the appropriate frameworks identified from the conceptual model (Step 2). This process allowed us to gauge how much of the conceptual model was supported by published literature.

Step 6: Research Gaps and Information Needs. The annotated bibliography and hypothetical frameworks were used to prepare syntheses (submodels) for major interactions related to elk on the northern range (e.g., elk-fire). These submodels were identified from the conceptual model. For each submodel, we reported the total number of papers reviewed and the distribution of their IP categories. Additionally, we identified strongly supported hypotheses, weakly supported hypotheses, and research gaps for each submodel. If relevant to elk ecology on the northern range, research findings from studies conducted outside YNP were also incorporated into each submodel synthesis. The ultimate result of this step was the identification of future research needs (research gaps) for each submodel.

Step 7: Research Prioritization. We developed a quantitative method to compare research gaps among submodels. This approach provided us with an empirical foundation on which to prioritize research needs. We calculated a research gap value (RGV) for each submodel based on 3 criteria: 1) total number of papers with IP values ≤ 4 within a submodel; 2) the mean IP of papers with IP values ≤ 4 within a submodel; and 3) the proportion of pathways addressed within a submodel. Within each of these categories, submodels were ranked relative to each other (e.g., if there were 10 submodels, they

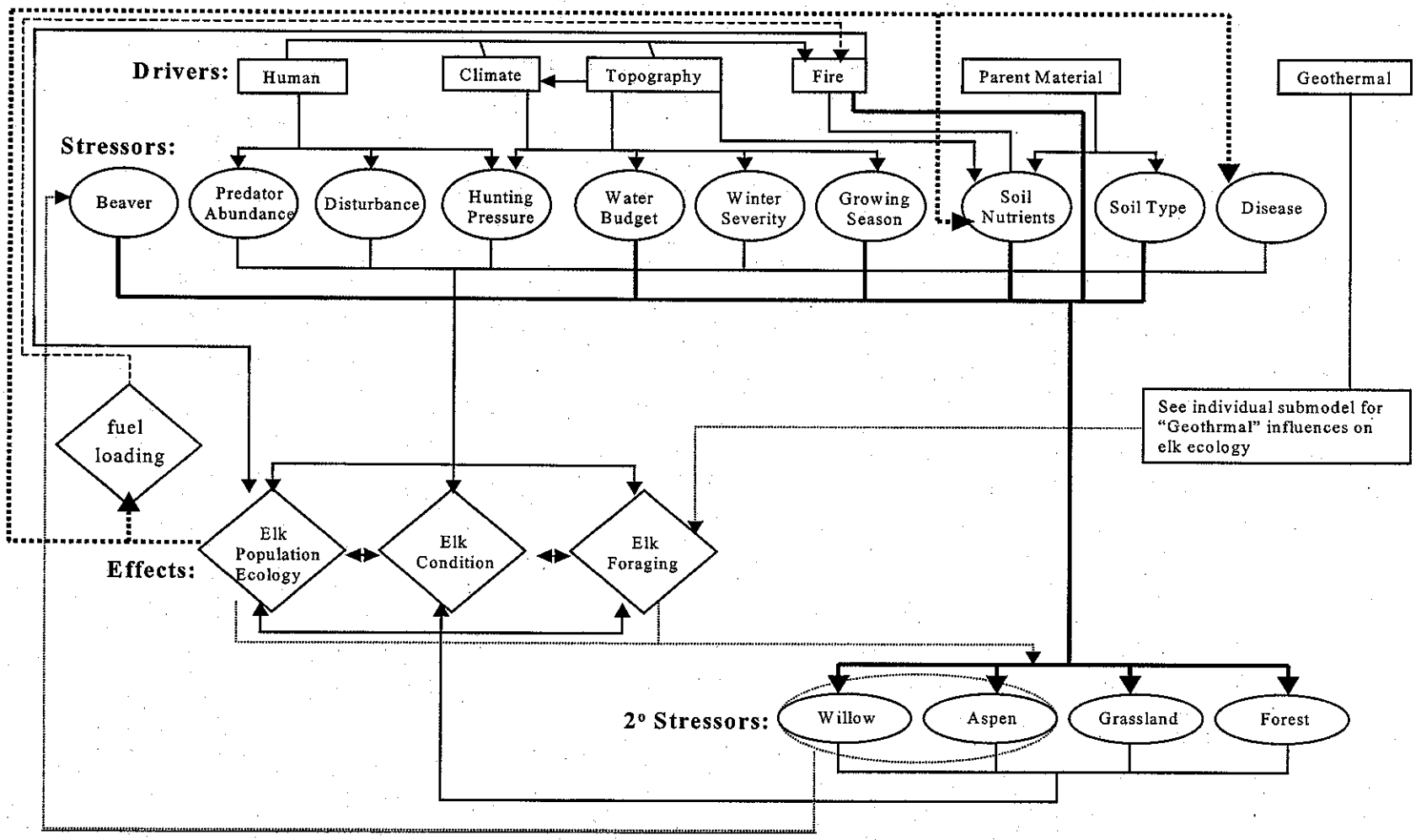
would have been ranked 1 through 10 with 10 assigned to the submodel with the poorest coverage (e.g., least number of papers). We then calculated a RGV for each submodel by summing the rankings across the three categories (e.g., $RGV_x = a_x + b_x + c_x$; where a_x = submodel x's ranking for total number of papers, b_x = submodel x's ranking for mean inferential power, and c_x = submodel x's ranking for the proportion of pathways addressed). We graphically displayed the ordination of the RGVs for all submodels on a one-dimensional figure with the y-axis labeled "research gaps".

To demonstrate potential integration of research gaps with management concerns, we generated an urgency value (URGV) for each submodel. The URGV was based on two criteria: 1) the temporal scale of a submodel, or simply, the speed at which ecological effects are realized (long-term (century) = 1, medium-term (decade) = 2, and short-term (annual) = 3); and 2) the degree to which a topic is a high profile park management issue (1 (high priority) through 5 (low priority)). We then calculated a URGV for each submodel by summing the values across these two categories (e.g., $URGV_x = a_x + b_x$; where a_x = submodel x's temporal score; and b_x = submodel x's management priority score. We subsequently used a 2-axes graph, with RGVs on the y-axis and URGVs on the x-axis, to visualize their relative relationships and determine research priorities. Finally, we calculated a priority score for each submodel by taking the product of the RGV and the URGV.

OVERALL FINDINGS

The initial efforts of this process resulted in several iterations of an elk-centric conceptual model for the northern range. The final iteration contained 6 drivers, 10 stressors, and 4 secondary stressors, all of which influenced elk population ecology, elk foraging, and/or elk condition (Fig. 1). It was this model for which the identification of research gaps and research prioritization was based. We reviewed and annotated 130 publications: 72 journal articles, 17 book chapters, and 41 non-peer reviewed National Park Service and technical reports). Fourteen submodels described in detail below were identified from the conceptual model. These included aspen, willow, grassland, forest, topography, climate, parent material, geothermal, fire, humans, predation, disease, beaver and competition. We identified research gaps within each submodel and quantified the relative inferential strength and scope of topics. Our findings revealed that with regard to elk in YNP, relations with beaver have yet to be scientifically addressed, while geothermal features/events, parent material, and topographic influences have been inadequately researched in comparison to other model components. In contrast, elk relations with grassland, aspen, coniferous forest, and fire have been relatively well studied in the GYE; the former topic having drawn considerable political attention in the 1990's, and the later 3 the result of opportunistic research that followed the 1988 fires. Our elk-centric model indicated those topics concerning beaver, disease, humans, predation, and competition should receive the highest research priority and those involving elk relations with grasslands, topography, parent material, and geothermal features/events should receive the least. In conclusion, we recommend elk-centric research priorities as identified through the application of this Comprehensive Rapid-assessment for Research Agenda Development.

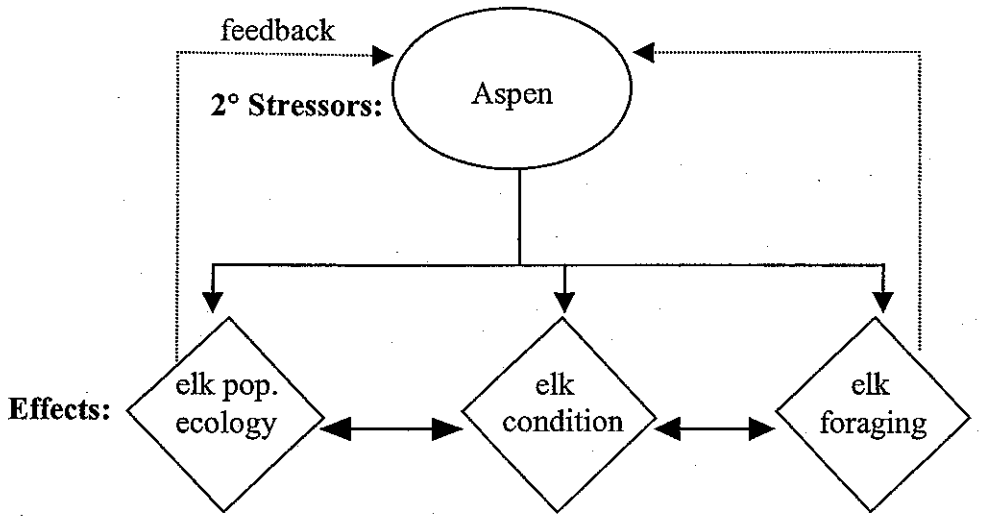
Figure 1. An elk-centric conceptual model illustrating the structure and function of Yellowstone's northern range.



SUBMODELS

Aspen/Elk Submodel. The following model depicts the direct and indirect interactions (pathways) that we identified between aspen and elk on the northern range.

Aspen/Elk Pathways

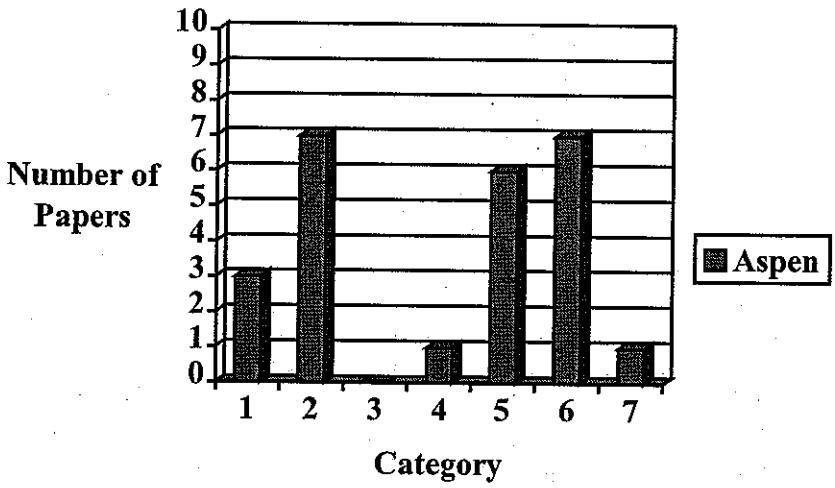


Synopsis of Reviewed Literature. We reviewed 25 papers and book chapters that addressed relationships between aspen and elk, abiotic influences on aspen, and other influences on aspen productivity and distribution (Chadde and Kay 1991, Christensen et al. 1988, Coughenour and Singer 1996b, Debyle 1979, Ellis et al. 1994, Huff and Varley 1999, Jackson 1993, Kay 1985, Kay 1993, Kay 1997, Kay 1998, Kay and Wagner 1994, Kay and Wagner 1996, Knight 1996, Knight and Wallace 1989, Renkin and Clark 1994, Renkin and Despain 1996a, Renkin and Despain 1996b, Ripple et al. 2001, Romme et al. 1995, Singer et al. 1998, Singer and Mack 1999, Singer and Norland 1994, Singer and Schoenecker 2003, Whitlock et al. 1991). Most of the papers (56%) were observational natural history or syntheses that lacked sampling design and were opportunistic or retrospective in nature (Fig. 4). However, some (n=10) papers suggested mechanistic explanations for patterns of aspen growth in the northern range via experimental (category 1) and observational (category 2) studies (Ellis et al. 1994, Kay 1985, Kay and Wagner 1996, Renkin et al. 1994, Renkin and Despain 1996a, Renkin and Despain 1996b, Ripple et al. 2001, Romme et al. 1995, Singer and Schoenecker 2003).

Although Singer and Norland (1994) found that aspen constituted less than 1% of elk diets, much of the literature on aspen regeneration and the potential effects of elk herbivory on the northern range focuses on the debate of whether elk are responsible for a reduction in tree-sized aspen (e.g., Kay 1985). Huff and Varley (1999) provided several scenarios that may have resulted in aspen historically growing to tree size including unique growing conditions, differential palatability after browsing, and lower browsing pressure resulting from elk population declines. The aspen debate is frequently coupled with the potential effects of elk herbivory on willow. The population dynamics of aspen

are different from those of willow, however, because aspen reproduction is facilitated by fire (DeByle 1979, Kay 1993) and aspen often inhabits upland sites.

Figure 4. Distribution of inferential categories for elk/aspen literature.



Preliminary analyses have suggested a top-down influence of wolves in facilitating aspen sucker growth in wet meadows (Ripple et al. 2001). Changes in elk spatial distribution in response to wolf pack distribution may release some aspen from herbivory and encourage regrowth to tree size. Elk appear to have the potential to limit aspen growth in YNP (Kay 1993, Dieni et al. 2000), however, the degree of reduction caused by elk browsing appears to be more a function of feeding location rather than elk abundance in a particular area (Ripple et al. 2001).

Reconciliation of Reviewed Literature and Pathways Linking Aspen and Elk Ecology. The following list identifies the major pathways and feedback loops linking aspen and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

2° Stressor →	**Ecological Effects**
Aspen	Elk Population Ecology
Aspen	Elk Condition
Aspen	Elk Foraging

Feedbacks

Elk Population Ecology →	Aspen
Elk Condition	Aspen
Elk Foraging	Aspen

Singer and Norland (1994) address the "Aspen → Elk Foraging" pathways. These authors reported that aspen constitutes less than 1 percent of northern range elk diets.

Nine reviewed papers addressed the "Elk Population Ecology/Foraging → Aspen" feedback loops (Ellis et al. 1994, Kay 1985, Kay and Wagner 1994, Renkin et al. 1994, Renkin and Despain 1996a, Ripple et al. 2001, Romme et al. 1995, Singer and Norland 1994, Singer and Schoenecker 2003,Whitlock et al. 1991), and others (categories 5-7) offered limited dicusssion (Chadde and Kay 1991, Huff and Varley 1999, Jackson 1993, Kay 1993, Kay 1997, Kay 1998, Kay and Wagner 1996, Knight and Wallace 1989). The literature regarding the effects of elk browsing on aspen growth is contradictory and confounded by the effects of other environmental factors such as fire and weather (Ellis et al. 1994, Christensen et al. 1988, Kay 1993, Renkin et al. 1994). Much of the debate focuses on the role of browsing in preventing aspen from developing to tree height over the past century, especially after wolves were eliminated from the system, and whether the size of the elk population has increased following the cessation of culling within YNP.

Singer and Schoenecker (2003) compared the ecosystem effects of ungulate herbivory on nitrogen cycling in Rocky Mountain National Park and YNP. They found that effects in short-willow and -aspen vegetation types fit the decelerating nutrient cycling scenario. Willow and aspen showed decreases in soil N mineralization rates, aboveground production, N pools and aboveground N.

Some authors contend that elk browsing alone has prevented aspen from growing to canopy height (Chadde and Kay 1991, Kay 1985, Kay 1997, Kay 1998, Kay and Wagner 1994, Kay and Wagner 1996). Only aspen sprouts that were underneath snowpack escaped browsing, suggesting that ungulate browsing is indeed intense and that accessible aspen sprouts are browsed in the winter (Romme et al. 1995). Renkin et al. (1994) reported that seedling survival was negatively correlated with browsing pressure. However, trampling may contribute more than browsing to aspen seedling mortality (Renkin et al. 1994).

In contrast, other authors have identified additional factors besides elk browsing that may, in part, contribute to the suppression of aspen growth and succession. Other factors that reduce aspen seedling growth and survival include spring flooding, intense fire, disease, intraspecific competition, and interspecific competition with lodgepole pine seedlings (Renkin et al. 1994, Renkin and Despain 1996a). The warmer, drier climate and suppression of fires during the past century may also be important in reducing aspen growth (Huff and Varley 1999, Romme et al. 1995). Renkin and Despain (1996b) attributed the inability of shrub aspen to develop into trees primarily to physical site conditions, such as moisture and soil type.

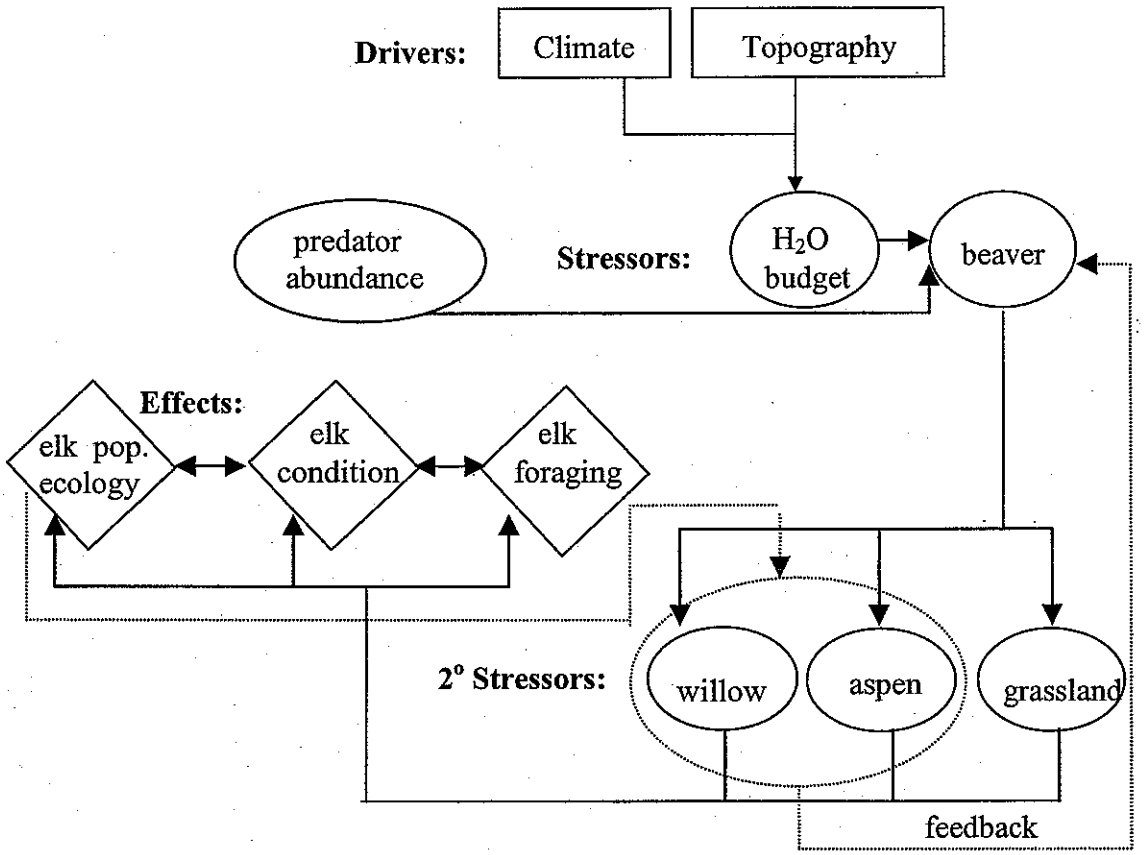
Following the 1988 fires, burned aspen sites responded quickly by root sprouting (Knight and Wallace 1989) and aspen seedlings were found in moderately burned and canopy burned areas (Ellis et al. 1994). During the 2 years after the 1988 fires, aspen sprout density was higher in burned than unburned stands. By 1991, however, no difference

between burned and unburned stands could be detected (Romme et al. 1995). Browsing by ungulates may increase following a fire because of increased forage availability and palatability (Knight and Wallace 1989). As a result, some authors maintain that increased growth post-fire is not sufficient to overcome ungulate browsing pressure and allow shrub aspen to grow into trees (Kay 1993, Kay and Wagner 1996). Indeed, Renkin and Despain (1996b) found that elk browsing influenced both sucker heights and age-class distribution. However, browsing had no effect on sucker density or mortality 5-7 years post-fire (Renkin and Despain 1996b).

The scope and intensity of the effect of elk on aspen are important to understand because, although aspen comprises a minor component of the vegetation communities on the northern range (Whitlock et al. 1991), it is a unique habitat type that supports high biodiversity. For example, intense browsing on aspen by elk was found to reduce habitat for songbirds (Jackson 1993). Reintroduced wolves may alter elk distribution, which in turn could reshape the vegetation structure of the northern range. Ripple et al. (2001) reported that aspen in high wolf-use areas experienced less elk use (as indexed by elk pellet counts). Aspen sucker heights were higher in high wolf-use areas than low wolf-use areas (Ripple et al. 2001).

Beaver/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between beaver and elk on the northern range.

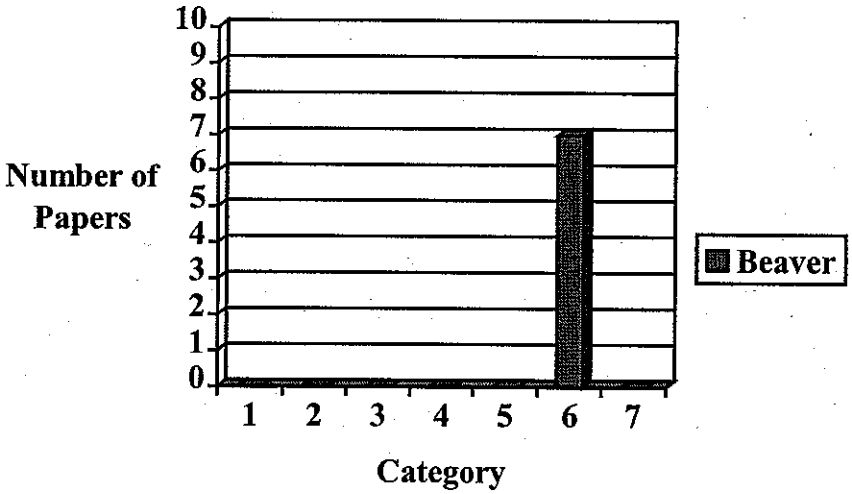
Beaver/Elk Pathways



Synopsis of Reviewed Literature. We found 7 papers that discussed beaver on the northern range (Chadde and Kay 1991, Huff and Varley 1999, Kay 1997, Kay 1998, Singer 1996a, Singer et al. 1994, Singer et al. 1997). These papers hypothesized that either: 1) increased elk numbers result in the decline and local extinction of beaver through competitive exclusion, or 2) decreased beaver numbers result in willow decline. The only category represented included papers based on observational natural history (Category 6) (Fig. 5). However, data from Singer (1996a) supported the hypothesis that beaver decline can contribute to willow decline in the northern range.

The beaver is often recognized as an ecological keystone due to its ability to modify habitats (Simberloff et al. 1999). Further, myriads of taxa are dependent on beaver for the maintenance of wetlands or seral communities that result after beaver abandon a site. It appears as though the ecological importance of beaver is no less in YNP. Without beaver, stream channels deepened, water tables dropped, and riparian vegetation was lost (Kay 1997). The decline of riparian plant communities not only impacts winter forage for ungulates, but also songbird breeding habitat (Jackson 1993).

Figure 5. Distribution of inferential categories for elk/beaver literature.



A synthesis of these few papers suggests that beavers create environmental conditions that foster willow growth and regeneration. In turn, beavers depend on willow for forage and dam building. Elk consume willow, and at high densities out-compete beaver for forage. Elk-induced beaver declines result in reduced willow growth and regeneration. Finally, continued browsing by elk results in reduced willow height, limited seed production, and complete loss of some willow communities. Is this relation unbalanced? Singer et al. (1998) suggested that the beaver decline in YNP may have exceeded a threshold for willow persistence and recruitment. While Singer et al. (1994) concluded that the proximate factor for low willow growth was herbivory by ungulates, they also suggested that drier conditions during the last 100 years and a decline in the YNP beaver population may partly explain willow decline.

Reconciliation of Reviewed Literature and Pathways Linking Beaver and Elk Ecology. The following list identifies the major pathways and feedback loops linking beaver and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor** →	**Ecological Effects**
Climate	Water Budget	Beaver
Topography	Water Budget	Beaver

Stressor →	**2° Stressor**
Predator abundance	Beaver

Stressor	→	2° Stressor	→	Ecological Effects
Beaver		Willow		Elk Population Ecology
Beaver		Willow		Elk Condition
Beaver		Willow		Elk Foraging
Beaver		Aspen		Elk Population Ecology
Beaver		Aspen		Elk Condition
Beaver		Aspen		Elk Foraging
Beaver		Grassland		Elk Population Ecology
Beaver		Grassland		Elk Condition
Beaver		Grassland		Elk Foraging

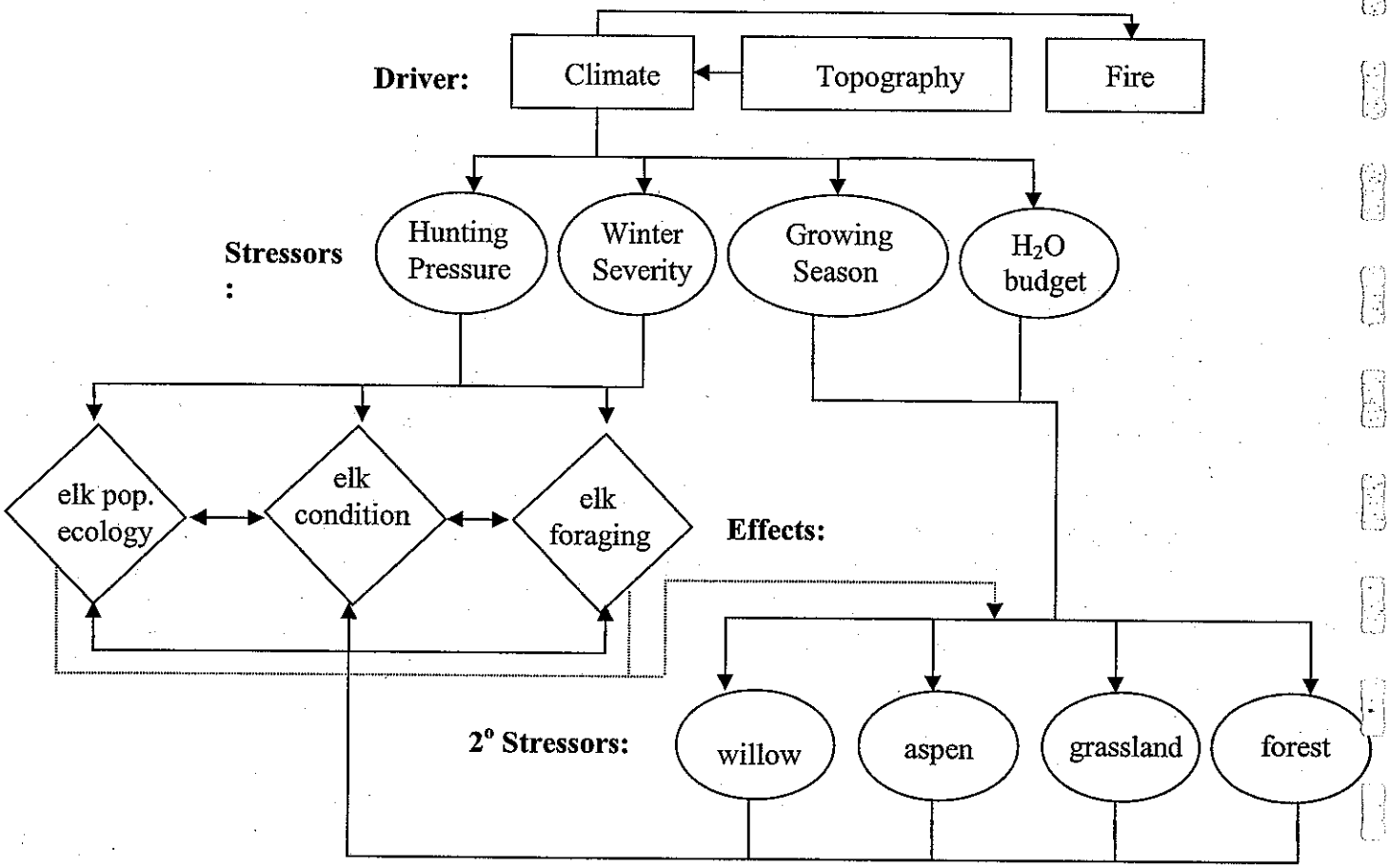
Feedbacks

Elk Population Ecology	Willow	Beaver
Elk Foraging	Willow	Beaver
Elk Population Ecology	Aspen	Beaver
Elk Foraging	Aspen	Beaver

None of the papers reviewed for the beaver submodel tested hypotheses relevant to the species role in the northern Yellowstone Ecosystem. However, a review of the natural history led several authors to suggest that beaver have been virtually eliminated and rendered ecologically nonfunctional from the northern range due to interspecific competition with elk (Chadde and Kay 1991, Kay 1997, Kay 1998, Singer et al. 1994).

Climate/Elk Submodel. The following model depicts the direct and indirect interactions (pathways) that we identified between climate and elk on the northern range.

Climate/Elk Pathways

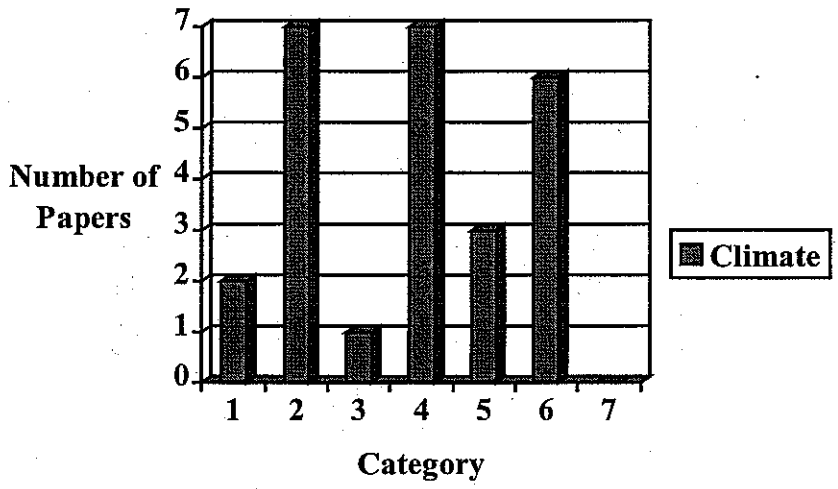


Reviewed Literature. We reviewed 26 papers that addressed climate-related issues on the northern range of YNP (Balling 1992, Coughenour 1994, Coughenour and Singer 1996a, Coughenour and Singer 1996b, Frank and McNaughton 1991, Frank et al. 1994, Kay 1985, Kay 1997, Kay and Wagner 1996, Reardon 1996, Romme and Turner 1991, Romme et al 1995, Shovic 1994, Singer 1996a, Singer et al. 1989, Singer et al. 1994, Singer and Cates 1995, Singer et al. 1998, Singer et al. 1998, Singer and Mack 1999, Stohlgren et al. 1999, Taper and Gogan 2002, Turner et al. 1997, Vales and Peek 1996, Wagner et al. 1995, Whitlock et al. 1991). Many of these papers dealt with the impacts of winter severity on over-winter elk survival, and issues related to drought and fire – phenomena that are certainly related to climate but can be studied over relatively short time periods. High inferential power was associated with 12 papers (categories 1 and 2, Fig. 6); however, climate per se was only indirectly implicated in these papers as a significant influence on ecological processes.

Over the course of human evolution, global climate has fluctuated as the result of continental drift, the Earth's orbital eccentricity, variation in solar radiation, changes in

ocean currents, and ice cap dynamics (Goudie 1992). In North America, prehistoric climatic cycles have been tied to human population dynamics and the disappearance of entire cultures (O'Brien 2001). Within the last 300 years, atmospheric changes caused by humans have become measurable on a global scale (Goudie 2000). During the 1800s, atmospheric carbon dioxide began a steady increase, apparently in response to the combustion of fossil fuels and deforestation (McNeill 2000). Similarly, atmospheric methane increased due to agriculture, livestock, garbage decomposition, and coal mining.

Figure 6. Distribution of inferential categories for elk/climate literature.



Regardless of the cause of global warming, climatic variation will have an influence on environmental conditions and biodiversity. Changes in species distribution, abundance, as well as community composition and biotic interactions have been attributed to climate change (Root and Schneider 2002). Biological communities within the bounds of YNP have been identified as particularly vulnerable to climate change (Balling et al. 1992, Koteen 2002). A recent warming trend suggests that YNP is becoming more arid (Balling et al. 1992, Turner et al. 1997). Warmer, drier conditions may facilitate more frequent large fires and reduce the distribution of forest cover as xeric conditions prevail. Though more non-forested habitat would be available to ungulates, herbaceous forage quality could decline because of reduced plant production and altered carbon:nitrogen ratios in vegetation as a result of drier conditions and higher atmospheric carbon dioxide levels (Romme and Turner 1991). Explanations of changes in YNP plant communities have been confounded by long-term trajectories in temperature and precipitation, and short-term weather patterns (Frank and McNaughton 1991, Romme and Turner 1991, Reardon 1996, Singer 1996).

Reconciliation of Reviewed Literature and Pathways Linking Climate and Elk Ecology. The following list identifies the major pathways and feedback loops linking climate and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or

pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor** →	**Ecological Effects**
Climate	Hunting Pressure	Elk Population Ecology
Climate	Hunting Pressure	Elk Condition
Climate	Hunting Pressure	Elk Foraging
Climate	Winter Severity	Elk Population Ecology
Climate	Winter Severity	Elk Condition
Climate	Winter Severity	Elk Foraging

Driver →	**Stressor** →	**2° Stressor** →	**Ecological Effects**
Climate	Growing Season	Willow	Elk Pop. Ecology
Climate	Growing Season	Willow	Elk Condition
Climate	Growing Season	Willow	Elk Foraging
Climate	Growing Season	Aspen	Elk Pop. Ecology
Climate	Growing Season	Aspen	Elk Condition
Climate	Growing Season	Aspen	Elk Foraging
Climate	Growing Season	grassland	Elk Pop. Ecology
Climate	Growing Season	grassland	Elk Condition
Climate	Growing Season	grassland	Elk Foraging
Climate	Growing Season	conifer forest	Elk Pop. Ecology
Climate	Growing Season	conifer forest	Elk Condition
Climate	Growing Season	conifer forest	Elk Foraging
Climate	Water Budget	Willow	Elk Pop. Ecology
Climate	Water Budget	Willow	Elk Condition
Climate	Water Budget	Willow	Elk Foraging
Climate	Water Budget	Aspen	Elk Pop. Ecology
Climate	Water Budget	Aspen	Elk Condition
Climate	Water Budget	Aspen	Elk Foraging
Climate	Water Budget	grassland	Elk Pop. Ecology
Climate	Water Budget	grassland	Elk Condition
Climate	Water Budget	grassland	Elk Foraging
Climate	Water Budget	conifer forest	Elk Pop. Ecology
Climate	Water Budget	conifer forest	Elk Condition
Climate	Water Budget	conifer forest	Elk Foraging

Three reviewed papers addressed the "Climate → Winter Severity → Elk Population Ecology/Condition/Foraging" pathways (Coughenour 1994, Coughenour and Singer 1996a, Coughenour and Singer 1996b). Snow accumulation limits the foraging area available to elk and influences elk distribution on the winter range (Coughenour and Singer 1996b). Severe winter conditions, especially in late winter, will deteriorate elk condition (Coughenour and Singer 1996b). Along with spatial and temporal distributions of forage and elk nutritional requirements, snow depth was used to model the elk carrying

capacity of the northern range (Coughenour 1994). In another modeling exercise, Coughenour and Singer (1996a) evaluated the effects of drought and deep snow on the winter 1988/89 die-off of elk.

Frank et al. (1994) addressed the "Climate → Growing Season → Grassland pathway." These authors hypothesized that variation in climate may produce significant inter-annual variability in nitrogen mineralization in the northern range's grassland ecosystem.

Coughenour and Singer (1996b) addressed the "Climate → Growing Season → Grassland → Elk Condition/Foraging pathways." These authors reported that early spring snowfall and, therefore, late snow melt and green-up delays the movement of elk to the summer range. Thus, early spring snowfall was hypothesized to reduce the time that elk can build up energy reserves on summer forage and contribute to higher adult elk mortality during the following winter.

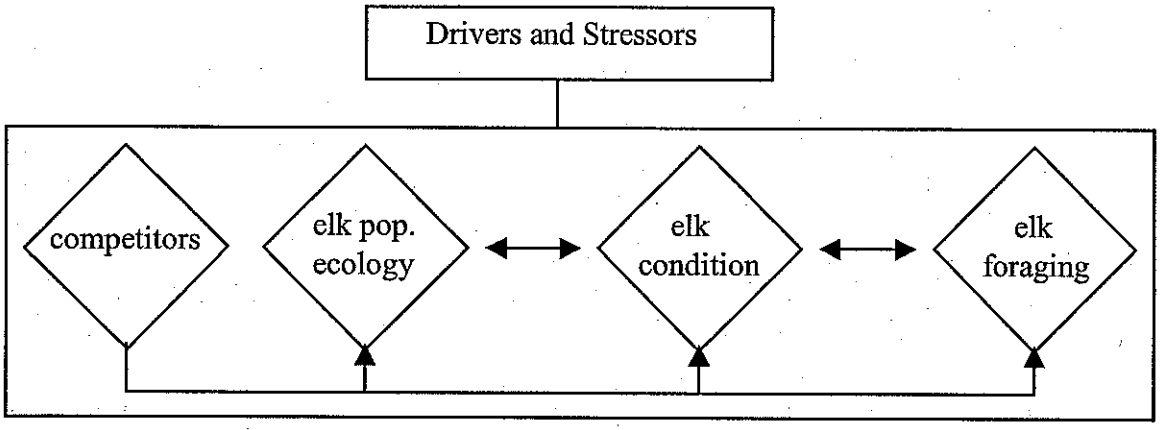
Six reviewed papers addressed the "Climate → Water Budget → Willow" pathway (Kay 1997, Singer 1996a, Singer et al. 1994, Singer and Cates 1995, Singer et al. 1998, Wagner et al.1995). Warmer and drier climatic conditions of the past century have contributed to reduced willow establishment (Singer 1996a, Singer et al. 1994, Singer and Cates 1995, Singer et al. 1998), although others contend that heavy browsing by an overpopulated elk herd, rather than long-term climatic and water table changes, is primarily responsible for the decline of willow establishment (Kay 1997, Wagner et al.1995).

Three reviewed papers addressed the "Climate → Water Budget → Aspen" pathway (Kay 1985, Kay and Wagner 1996, Romme et al. 1995). Romme et al. (1995) suggested environmental conditions (e.g., wetter climate and recent fires) and biological conditions (e.g., fewer ungulates, more predators including wolves) during 1870-1890 allowed the establishment of present-day aspen stands. However, others contend that climatic factors are not important for aspen recruitment and ungulates must be excluded to attain tree-sized aspen (Kay 1985, Kay and Wagner 1996).

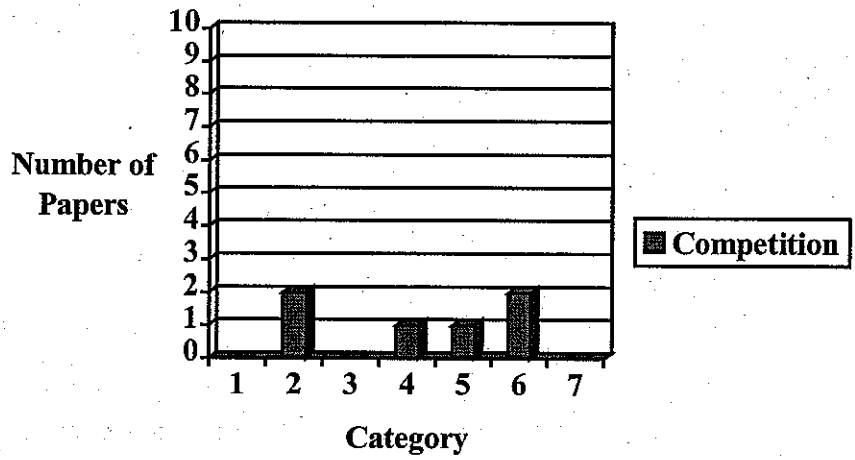
Four reviewed papers addressed the "Climate → Water Budget → VEGETATION → Elk Pop/Condition/Foraging" pathways (Coughenour and Singer 1996a, Taper and Gogan 2002, Romme and Turner 1991, Vales and Peek 1996). Climate change (e.g., temperature and moisture) can affect the distribution and abundance of grassland communities and forested habitats, leading to a complementary change in ungulate distribution and populations (Romme and Turner 1991). The climatic events of 1988/89 provide a poignant example of direct and indirect climate effects on elk forage, body condition, and survival. Summer drought conditions of 1988 provided poor forage for elk and, combined with the deep snowfall in the winter of 1988/89, led to the dramatic decline of elk during that winter (Coughenour and Singer 1996a, Taper and Gogan 2002, Vales and Peek 1996).

Competition/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified related to competition between elk and other herbivores on the northern range.

Competitor/Elk Pathways



Synopsis of Reviewed Literature. We found 5 papers and 1 book chapter that mentioned competition between elk and other herbivores on the northern range of YNP (Chadde and Kay 1991, Coughenour and Singer 1996b, Ferrari and Garrott 2002, Houston 1976, Singer and Norland 1974, Tracy and McNaughton 1995). Three of these were data-based treatments without statistical/inferential power that proposed mechanistic explanations (n=1; Category 4), or were based on observational natural history (n=2; Category 6) (Fig. 7). One study (Singer and Norland 1994) utilized a descriptive approach with high inferential power that partially supported the hypothesis that increases in the number of elk would result in increased competition among ungulates on the northern range.



Additionally, Ferrari and Garrott (2002) utilized a descriptive approach with high inferential power to examine habitat overlap between elk and bison in the Madison Firehole region. Competition defined ecologically is that which occurs when two or more species contend for a commonly used resource, resulting in the decrease in fitness

of at least one species (Begon and Mortimer 1986). Close coexistence among related species can lead to competition if resources become limiting (Pianka 1974), and can result in a co-evolutionary response of niche partitioning (Jenkins and Wright 1988). Thus, interspecific competition can be important in shaping the distribution (Wiens 1979) and spacing (Diamond 1978, Wiens and Rotenburg 1981) of species within an ecological community.

Among sympatric ungulates, morphological, physiological, and behavioral differences have evolved to allow habitat and diet selection that minimizes interspecific competition (Geist 1974). Although larger ungulates are typically dominant over smaller ones, interference competition is uncommon. Dietary overlap has been the most frequently used indicator of interspecific competition among sympatric cervids (Hanley and Hanley 1982, Leslie et al. 1984, Gogan and Barrett, 1995, Kirchoff and Larsen 1998). Because Yellowstone supports a large elk population and a diverse assemblage of other ungulate species, both intraspecific and interspecific competition are important in shaping the population dynamics of Yellowstone's ungulates. In most cases, dietary overlap among ungulates, and thus the potential for competition, is greatest in the winter when available forage becomes limited. YNP's current policy of natural regulation is based upon the hypothesis that competition for limited forage resources results in density-dependent, self regulation of Yellowstone's large mammal populations (Cole 1971).

One of the premises behind successful natural regulation policy is that no single ungulate species in the park will significantly reduce or eliminate another (Cole 1971, Houston 1976). To date, only one study has attempted to examine potential competition among Yellowstone's ungulates (Singer and Norland 1994). These authors examined niche relations among elk, bison, mule deer, pronghorn, and bighorn sheep on the northern winter range of YNP, and found that elk and bighorn exhibited a degree of habitat and dietary overlap that suggested the potential for interspecific competition. Additionally, these findings suggested that increases in the use of sagebrush communities by bighorn may reflect interspecific competition with elk.

Some researchers argue that interspecific competition due to an increasing elk population has virtually eliminated beaver from the northern range (Chadde and Kay 1991). The fact that little empirical evidence exists regarding competition between Yellowstone's ungulates is not to say it does not occur. It may take several decades before competitive exclusion becomes apparent. Conversely, competition between species may not lead to the exclusion of one of them (Stiling 1992). Rather, species may modify behavior or feeding habits to minimize competition.

<u>Reconciliation of Reviewed Literature and Pathways linking Competition and Elk Ecology.</u> The following list identifies the major pathways and feedback loops linking elk and their competitors on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Stressor →	Ecological Effects
Competitors	Elk Population Ecology
Competitors	Elk Condition
Competitors	Elk Foraging

FEEDBACKS

Elk Population	Competitors
Elk Condition	Competitors
Elk Foraging	Competitors

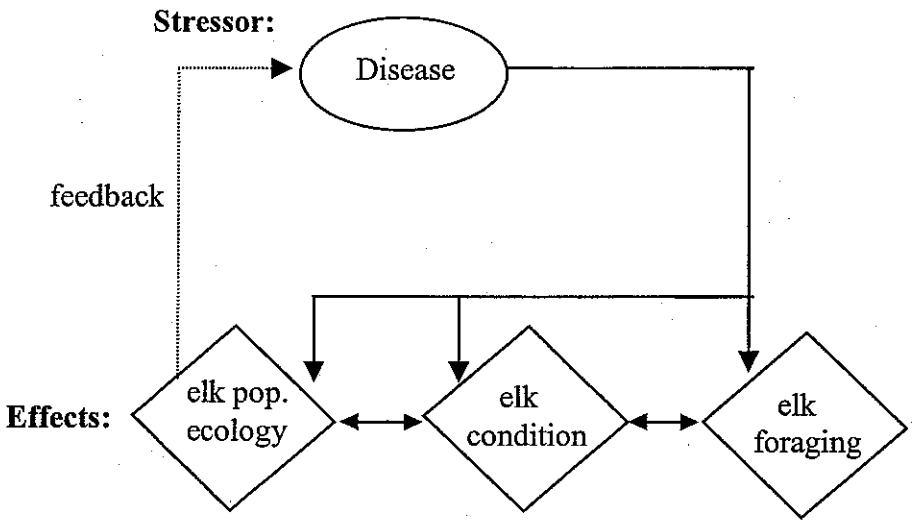
Singer and Norland (1994) addressed the "Competitors → Elk Foraging" and "Competitors → Elk Population Ecology" pathways and the "Elk Population→ Competitors" and "Elk Foraging → Competitors" feedback loops. These authors found that elk and bighorn sheep were most likely among the park's ungulates to be interspecifically competitive. Regardless, the number of YNP's ungulates tripled during the study period.

Coughenour and Singer (1996) addressed the "Competitors → Elk Population Ecology" pathway and suggested that although there is density-dependent competition for food, density-independent fluctuations in forage supply and forage availability prevent the population from attaining a static equilibrium.

Ferrari and Garrott (2002) addressed the "Competitors → Elk Population Ecology" pathway and found that increased numbers of bison and subsequent changes in their winter distribution promote a high degree of overlap between bison and elk in the Madison-Firehole winter range.

Disease/Elk Submodel. The following model depicts the direct and indirect interactions (pathways) that we identified between disease and elk on the northern range.

Disease/Elk Pathways



Synopsis of Reviewed Literature. We found 12 papers and book chapters that addressed the influence of diseases and parasites on elk in YNP (Aguirre and Starkey 1994, Berger and Cain 1999, Bergstrom and Robbins 1979, Dobson and Meagher 1996, Ferrari and Garrott 2002, Houston 1978, Lemke et al. 1998, Margolin and Jolley 1979, Meagher and Meyer 1994, Thompson and Henderson 1998, Thorne et al. 1979, Worley 1979)(Fig. 8). Most of the papers focused on historical and pathological aspects of brucellosis and its potential to limit the YNP elk herd.

Brucellosis appears to be maintained by large winter concentrations of elk and interactions with infected bison (Dobson and Meagher 1996, but see Ferrari and Garrott 2002). Although infection rates in elk are lower than in bison, the greater abundance of the former may make them more likely to spread the disease to cattle (Dobson and Meagher 1996). Only 7% of elk winter range is occupied by bison, which may explain the low infection rate in elk (Dobson and Meagher 1996). The lungworm (*Dictyocaulus viviparous*) and *Sarcocystis* spp. can cause considerable mortality, especially in younger animals (Bergstrom and Robbins 1979). Most other parasites and diseases do not appear to limit elk herds in YNP.

Although our understanding of the role of infectious diseases in the regulation of host wildlife population abundance and genetic diversity is incomplete at best (Gulland 1995), a variety of pathogens are known to have been important selective forces on human populations (McNeill 1976). Whereas contemporary humans have largely escaped the mass mortalities associated with a variety of pathogens, they have been instrumental in the transport and naturalization of diseases that are problematic for many native wildlife populations (Cunningham 1996). Some well-known examples of these include avian

malaria in Hawaii, rinderpest in Africa, and brucellosis in North America (Warner 1968, Plowright 1982, Gaydos and Corn 2001).

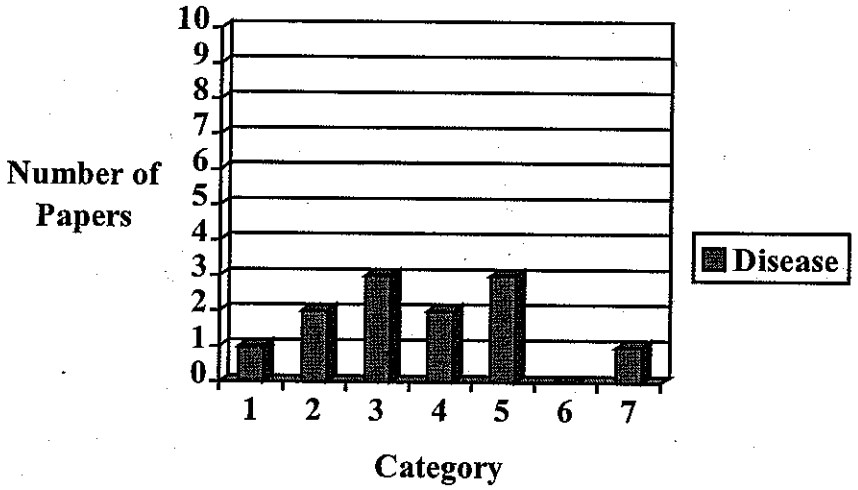


Figure 8. Distribution of inferential categories for elk/disease literature.

Whereas conservation programs have increasingly targeted endangered species with disease and parasite research, the most aggressive programs involve wildlife pathogens that directly influence humans and their livestock (Gulland 1995). This situation prevails in Yellowstone National Park where introduced brucellosis occurs in bison and elk that migrate in and out of the park and that might interact with domestic livestock on public and private ranges (Dobson and Meagher 1996). Although other diseases and parasites are of interest or have the potential to affect conservation programs in YNP, none has been as controversial or costly as brucellosis. However, increasing outbreaks of chronic wasting disease (CWD) and the resulting public concern (Williams et al. 2002) may supercede brucellosis as a management concern at YNP, especially if outbreaks begin to occur near or in the park.

Reconciliation of Reviewed Literature and Pathways linking Disease and Elk Ecology. The following list identifies the major pathways and feedback loops linking disease and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Stressor →	**Ecological Effects**
Disease	Elk Population Ecology
Disease	Elk Condition
Diease	Elk Foraging

Feedbacks

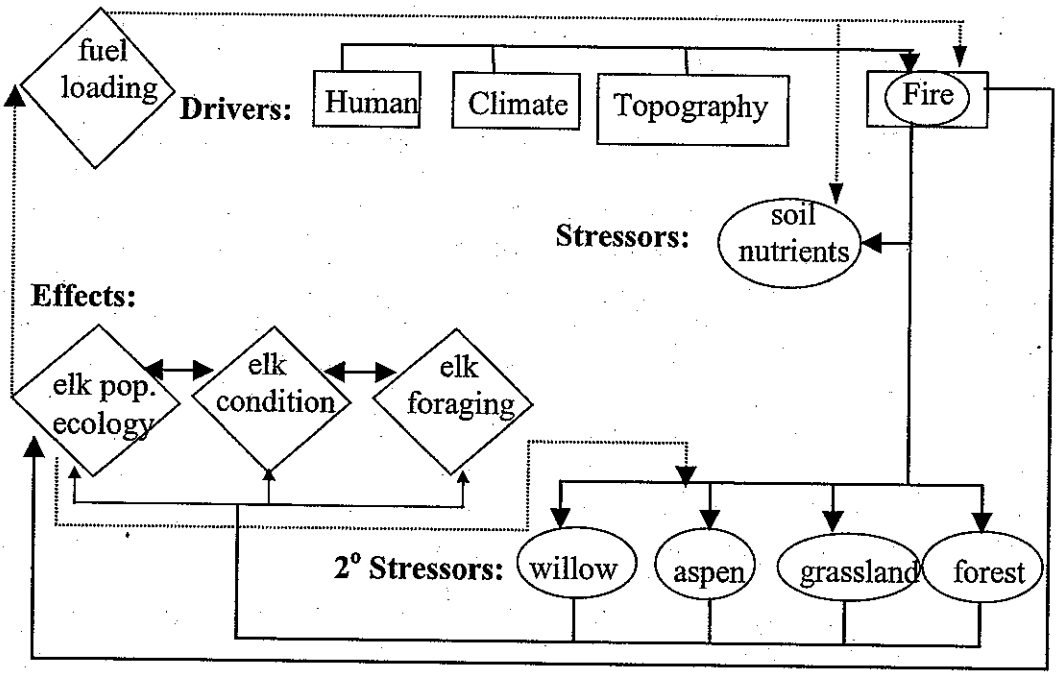
Elk Population Ecology Disease

A number of authors (Berger and Cain 1999, Bergstrom and Robbins 1979, Dobson and Meagher 1996, Houston 1978, Lemke et al. 1998, Margolin and Jolly, 1979 Thorne et al. 1979, Worley 1979) address the "Disease → Elk Population Ecology" pathway. Their findings suggest that brucellosis may limit elk population growth, and that the abundant elk herd provides a potential source of transmission for this disease to other ungulates, including domestic livestock. Ferrari and Garrott (2002) addressed concerns that increasing range overlap of bison and elk will lead to higher interspecific transmission rates of brucellosis between these two species. They concluded that despite high levels of commingling between elk and bison on winter range, the 3% seroprevalence rate in the Madison elk herd suggests that interspecies transmission of brucellosis from bison to elk in the Madison-Firehole area is low and comparable to populations of elk that do not interact with bison. Margolin and Jolly (1979) found that elk carcasses are a potential source of transmission of *Sarcocystis* to domestic dogs.

Bergstrom and Robbins (1979), Houston (1978), and Worley (1979) addressed the "Disease → Elk Condition" pathway. Houston (1979) suggested that most elk mortality was the result of the interaction between disease, parasites, and predators. Worley (1979) found that elk are host to at least 27 parasites, of which only one, lungworm *(Dictyocaulus viviparous)*, was important to elk population dynamics. Bergstrom and Robbins (1979) found that lungworm infection rates varied seasonally and by age in elk and suggested that lungworm infection rates may affect seasonal migration patterns.

Fire/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between fire and elk on the northern range.

Fire/Elk Pathways

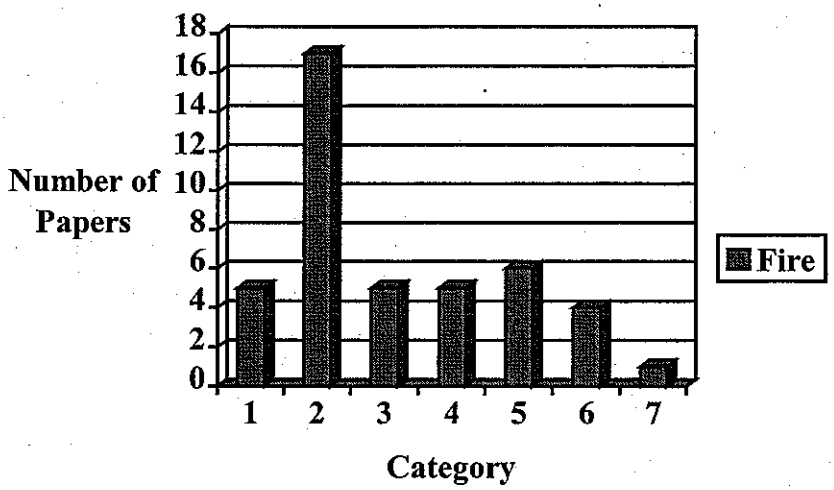


We reviewed 43 journal articles, book chapters, and agency reports that addressed influences of fire on elk and its habitat (Balling et al. 1992, Boyce and Merrill 1996, Christensen et al. 1988, Coughenour and Singer 1996a, DelGiudice and Singer 1996, Despain et al. 1996, Ellis et al. 1994, Farnes 1996, French and French 1996, Hobbs 1996, Huff and Varley 1999, Jakubas et al. 1994, Kay 1985, Kay 1993, Kay and Wagner 1994, Kay and Wagner 1996, Knight 1996, Knight and Wallace 1989, Noland et al. 1996, Pearson et al. 1995, Renkin et al. 1994, Renkin and Despain 1996a, Renkin and Despain 1996b, Romme and Knight 1982, Romme et al. 1995, Singer 1991, Singer et al. 1989, Singer and Schullery 1989, Singer and Harter 1996, Singer et al. 1997, Singer et al. 1998, Singer and Mack 1999, Taper and Gogan 2002, Tracy and McNaughton 1996, Turner et al. 1994a, Turner et al. 1994b, Turner et al. 1994c, Turner et al. 1994d, Turner et al. 1997, Vales and Peek 1996, VanDyke et al. 1991, VanDyke et al. 1996, Wu et al. 1996). Most (n=25) fire-related papers were opportunistic research associated with the 1988 fires. The category with the greatest representation (n=17) were those papers that utilized a descriptive approach with a priori sampling designs to provide mechanistic explanations of a phenomenon or process (category 2) (Fig. 9).

Recent climate change has caused increased temperatures in YNP during the fire season, and decreased precipitation and drought in other seasons resulting in increased aridity and enhanced fire potential (Balling et al. 1992). Although fire has been a persistent influence throughout the post-Pleistocene GYE, stand-replacing fires, such as those in 1988, have

typically occurred at intervals of 150-300 years (Balling et al. 1992). The scale and intensity of the Yellowstone fires provided a unique opportunity for examining the immediate effects and post-fire responses of the park's flora and fauna (Christensen 1988). The 1988 fire burned portions of 700,000 acres and subsequently was recognized as a driving force on landscape and biotic structure in the GYE (Romme and Despain 1989). For example, 25-30% of YNP was affected in 1988 by crown fires that greatly modified forest physiognomy (Knight and Wallace 1989).

Figure 9. Distribution of inferential categories for elk/fire literature.



Disturbances such as catastrophic fires can dramatically shift landscape dynamics (Turner et al. 1994a). An interaction of fire intensity, fire extent, pre-fire community, and geography affects the pattern of succession following fire (Turner et al. 1997). For example, plants producing volatile compounds in woody material may deter herbivory, but can lead to increased fuel loads and a greater likelihood of crown fires (Hobbs 1996). Temporal and spatial patterns of fire may have an influence on plant recolonization and survival (Turner et al. 1994c). Fires can affect movements and promote learned responses of ungulates to burned areas (Van Dyke et al. 1991), which in turn can alter foraging patterns that influence productivity and development of vegetation (Knight and Wallace 1989).

Several findings indicated preferential use of burned areas by elk (Pearson et al. 1995, Singer and Harter 1996, Tracy and McNaughton 1996), and that burned areas were good predictors of grazing intensity (Pearson et al. 1995). Conversely, others found elk habitat use in YNP was similar to that found in unburned areas (Norland et al. 1996). Singer and Harter (1996) suggested that burned areas may enhance the foraging efficiency of elk. However, Norland et al. (1996) found that elk diets did not increase in diversity or shift to less palatable plants as predicted by others (Singer et. al 1989). Fire increased the nutritional quality and digestibility of grasses in the GYE and facilitated elk consumption during the initial years after burning (Van Dyke et al. 1991, Norland et al. 1996, Singer

and Harter 1996, Tracy and McNaughton 1996). Graminoid and forb production increased and sagebrush (*Artemisia* spp.) production decreased from 1-5 years post-fire, and peak elk use occurred between 1-4 years post-fire (Van Dyke et al. 1996). Elk use was highest in areas where sagebrush was slow to reestablish following fire (Van Dyke et al. 1996).

Kay (1985) suggested that aspen is a successional species maintained not by fire but by elk. All aspen seedlings observed in GTNP and YNP from 1989 through 1991were associated with bare mineral soil, ash, and absence of competing vegetation following wildfires (Kay 1993). Ash generated from fires enhanced soil moisture holding capacity and retention and thereby contributed to successful aspen establishment (Renkin et al. 1994). Aspen are not necessarily predisposed to prolific growth following fire (Renkin and Despain 1996b). However, optimal growth response of aspen occurs in clones that occupy optimal sites, with pre-burn stem basal area and total root biomass of aspen being important factors determining growth (Renkin and Despain 1996b). Density of aspen sprouts was initially greater in burned versus unburned stands in 1990 (2 yr post-burn), but approached the density of unburned stands by fall 1991. Browsing intensity of aspen did not increase in burned areas nor was it related to the age of sprouts (Romme et al. 1995). Extensive fires may stimulate prolific aspen sprouting and allow some stems to escape browsing and grow beyond shrub stature (Renkin and Despain 1996a).

While elk did not negatively influence high elevation aspen seedling growth 5 years post-germination, at low elevations, elk browsing and trampling was found to maintain aspen seedlings at reduced heights (Renkin and Despain 1996a). From 1989 to 1991, average height of aspen seedlings declined from 58 cm to 47 cm, and by 1991, all aspen seedlings showed signs of repeated ungulate winter browsing (Kay 1993). Fires did not stimulate shrub-aspen height growth, stem density, or clonal spread, because of ungulate browsing (Kay and Wagner 1996, Knight 1996). Fire severity and prefire stand composition control and favor regeneration of lodgepole pine (Ellis et al. 1994, Despain et al. 1996), thus preferential browsing of aspen by elk increases the likelihood of eventual displacement of aspen by lodgepole pine in burned areas (Renkin and Despain 1996a).

New willow sprouts are important food for elk and other ungulates in burned riparian areas (Knight 1996). After fire, willow biomass, protein and digestibility increase, but stature does not (Norland et al. 1996). Ungulate herbivory increased on burned willow which were shorter 3 years post-fire than unburned willow (Norland et al. 1996).

Elk behavior was only slightly modified by wild fires, and <1% of the YNP elk population died as a result of the 1988 fires (Singer and Schullery 1989, French and French 1996). Most fire-related elk mortality was caused by smoke inhalation before the arrival of fire fronts (French and French 1996). Twelve of 20 radio-collared elk altered their movements in response to the 1988 fires, and some traveled to winter range several weeks earlier than the previous year (Vales and Peek 1996). The combined effects of drought and deep snow during the winter following the 1988 fires reduced the availability and quality of forage (Coughenour and Singer 1996a, Vales and Peek 1996), resulted in decreased survival of elk calves, and caused a 38-43% reduction of the YNP elk herd

(Singer et al. 1989, Singer et al. 1997). The fires, drought, and severe winter of 1988 likely contributed to the subsequent production of underweight elk calves and doubling of predation on elk calves during the summer of 1989 (Singer et al. 1997). Nonetheless, elk survival increased during the winter of 1989-90 (DelGiudice and Singer 1996) and population recovery was complete by 1993 (Knight 1996).

Population models suggest that winter mortality of elk would have been 7% lower without the 1988 fires and that winter severity and high elk densities were the primary factors that contributed to increased elk mortality the following winter (Wu et al. 1996, Taper and Gogan 2002). Models also suggest that the spatial pattern of burns can affect elk winter survival (Turner et al. 1994d, Wu et al. 1996). Elk survivorship was lower when fires were small and patchy rather than clumped or large and contiguous in non-critical winter habitat (Turner et al. 1994d, Wu et al. 1996). Vales and Peek (1996) found a positive correlation between the percentage of elk mortality and the burned area of winter range, with adult bulls most susceptible due to home range fidelity during the rut.

Apparently, the 1988 fires did not cause post-fire elk population declines, but instead resulted in habitat improvements and subsequent increases in the YNP elk population (Christensen et al. 1988, Singer et al. 1989, Singer 1991, Van Dyke et al. 1991, Boyce and Merrill 1996, Singer and Mack 1999). Regardless, the long-term effects of fire on GYE plant and animal communities remain to be fully understood. Whereas the fires of 1988 provided an impromptu opportunity to examine widespread and dramatic fire influences, future experimental work will be needed to fully understand its complex role in this landscape.

Reconciliation of Reviewed Literature and Pathways linking Fire and Elk Ecology. The following list identifies the major pathways and feedback loops linking fire and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that were placed in categories 1 through 4. Unshaded pathways or pathway segments were either not addressed in the reviewed literature or were only discussed in papers placed in categories 5 through 7.

Driver →	**Driver**
Human	Fire
Climate	Fire
Topography	Fire

Driver →	**Ecological Effects**
Fire	Elk Population Ecology

Driver →	**Stressor**	**→**	**Ecological**	**Effects**
Fire	Willow		Elk Population Ecology	
Fire	Willow		Elk Condition	
Fire	Willow		Elk Foraging	
Fire	Aspen		Elk Population Ecology	

Fire	Aspen	Elk Condition
Fire	Aspen	Elk Foraging

Fire	Grassland	Elk Population Ecology
Fire	Grassland	Elk Condition
Fire	Grassland	Elk Foraging

Fire	Forest	Elk Population Ecology
Fire	Forest	Elk Condition
Fire	Forest	Elk Foraging

Driver →	**Stressor**	**→ 2° Stressor**	**→ Ecological Effects**
Fire	Soil Nutrients	Willow	Elk Population Ecology
Fire	Soil Nutrients	Willow	Elk Condition
Fire	Soil Nutrients	Willow	Elk Foraging
Fire	Soil Nutrients	Aspen	Elk Population Ecology
Fire	Soil Nutrients	Aspen	Elk Condition
Fire	Soil Nutrients	Aspen	Elk Foraging
Fire	Soil Nutrients	Grassland	Elk Population Ecology
Fire	Soil Nutrients	Grassland	Elk Condition
Fire	Soil Nutrients	Grassland	Elk Foraging
Fire	Soil Nutrients	Forest	Elk Population Ecology
Fire	Soil Nutrients	Forest	Elk Condition
Fire	Soil Nutrients	Forest	Elk Foraging

Feedbacks

Elk Population Ecology	→	Fuel Loading	→	Fire		
Elk Population Ecology	→	Fuel Loading	→	Fire	→	Soil Nutrients

French and French (1996) and Vales and Peek (1996) addressed the "Fire → Elk Population Ecology" pathway. French and French (1996) found that elk exhibited indifferent behavioral responses to fire, and that fires were responsible for causing the deaths of less than 1% of the elk herd; the majority of which were caused by smoke inhalation. Vales and Peek (1996) found no shifts in homeranges for 12 of 20 radio-collared elk in response to the 1988 fires.

Norland et al. (1996) addressed the "Fire → Willow" pathway and found that fires caused increased production and nutritional quality in willow.

Coughenour and Singer (1996a) addressed the "Fire → Willow → Elk Population Ecology" pathway. Their modeling results indicated that, following the fires of 1988, changes in vegetation, including willow, would cause an initial decrease in ungulates, followed by a 10-15% increase in population 15-25 years post-fire.

Kay (1985) and Kay and Wagner (1996) addressed the "Fire → Aspen" pathway and suggested that based on historical photographs, overabundant ungulates were responsible

for suppressing aspen growth and that fire played an insignificant role in stimulating aspen growth.

Several authors addressed the "Fire → Aspen → Elk Foraging" pathway (Renkin et al. 1994, Renkin and Despain 1996a, and Renkin and Despain 1996b). Renkin et al. (1994) found that aspen seedling establishment and subsequent growth occurred post-fire, but repeated elk browsing curtailed further growth. Renkin and Despain (1996a) found that elk did not negatively impact aspen growth 5-7 years after the 1988 fires at elevations of 1800-2300m. Another study suggested that elk were found to influence age-class distribution of aspen of aspen seedlings, but not mortality or density (Renkin and Despain 1996b).

Jakubas et al. (1994) addressed the "Fire → Forest→ Elk Foraging" pathway to determine wether the 1988 fires improved the overall nutritional quality of lodgepole pine by altering the chemical composition and digestibility of the bark. They found that burned lodgepole pine bark was more digestible and contained more crude protein and less secondary metabolites than that of unburned trees.

Norland et al. (1994c) addressed the "Fire → Grassland" pathway and found that bunchgrass production and nutritional content were unchanged by the 1988 fires.

Multiple studies addressed the "Fire → Grassland → Elk Population Ecology" pathway (Boyce and Merrill 1996, Coughenour and Singer 1996a, Romme and Knight 1982, Singer et al. 1997, Taper and Gogan 2002, Turner et al. 1994b, and Wu et al. 1996). Romme and Knight (1982) suggested that elk population fluctuates with grassland availability. Boyce and Merrill (1996) and Coughenour and Singer (1996a) predicted that elk populations would increase following the 1988 fires due to increased availability of forage. In fact, an unusually severe winter coupled with the 1988 fires contributed to an elk population decline during the winter of 1988-89 (Turner et al. 1994d). Models suggested that fires were responsible for a 7% increase in calf mortality (Wu et al. 1996). However, elk population increased following the 1988 fires (Taper and Gogan 2002) likely in response to increased biomass, digestibility, and nutritional content of grasslands (Singer et al. 1997).

Several authors addressed the "Fire → Grassland → Elk Foraging" pathway (Norland et al. 1996, Pearson et al. 1995, Singer et al. 1989, Singer and Harter 1996, Vales and Peek 1996, Van Dyke et al. 1991, Van Dyke et al. 1996). Vales and Peek (1996) found that elk had diets with fewer forbs and more fiber post-fire than the year before. Norland et al. (1996) found that elk did not concentrate in burned areas following the 1988 fires, nor did the diversity of their diet shift toward more palatable plants. In contrast, others found that elk concentrated in burned areas (Pearson et al. 1995, Singer and Harter 1996), and had increased diversity and palatability of grasses in their diet (Singer et al. 1989, Singer and Harter 1996). Post-fire use of grasslands by elk was found to be most beneficial during the first five years (Van Dyke et al. 1991), with peak use occurring 1-4 years afterward during a period of increased graminoid and forb production (Van Dyke et al. 1996).

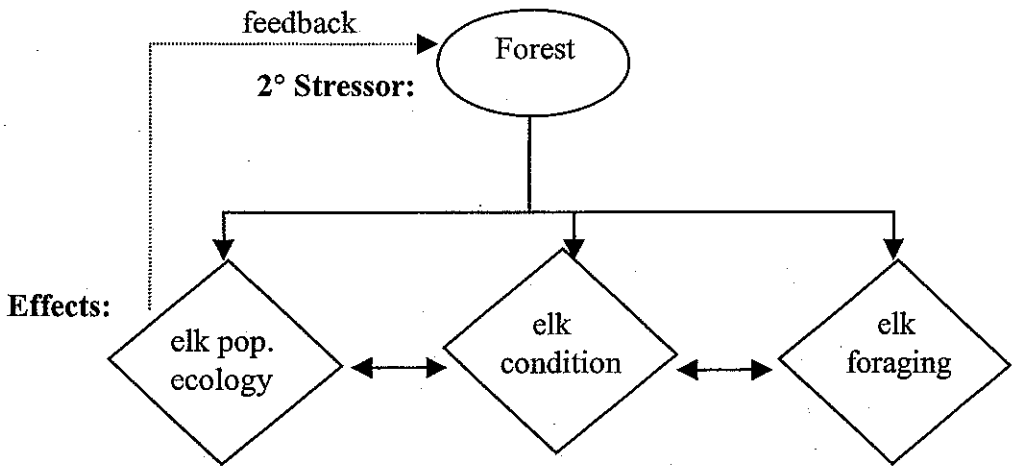
DelGiudice et al. (1996) addressed the "Fire → Soil Nutrients → Grassland → Elk Population Ecology" pathway and suggested that high post-fire ungulate:carbon ratios could reduce elk survival and reproduction.

A number of authors addressed the " Fire → Coniferous Forest" pathway (Balling et al. 1992, Despain et al. 1996, Ellis et al. 1994, Turner et al. 1994c, Turner et al. 1997). Balling et al. (1992) suggested that increased temperature and aridity during the past century have predisposed YNP to fire. Fire can alter landscape heterogeneity and vegetation patterns as a function of its intensity, distribution, and duration (Ellis et al. 1994, Turner et al. 1994c). Repeated fires can increase grassland:forest ratios (Turner et al. 1997), and alter forest communities by favoring serotinous species and causing mortality of non-serotinous species (Despain et al. 1996) through alteration of canopy seedbanks (Turner et al. 1994c).

Renkin et al. (1994) addressed the "Fire → Coniferous Forest → Elk Foraging" pathway and found that post-fire lodgepole pine seedlings were not adversely affected by elk broswing.

Forest/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between forest and elk on the northern range.

Forest/Elk Pathways



Synopsis of Reviewed Literature. We reviewed 15 papers that addressed forest/elk relationships and abiotic and other influences on forest productivity and distribution (Balling et al. 1992, Cassier et al. 1992, Christensen et al. 1988, Despain et al. 1996, Ellis et al. 1994, Farnes 1996, Jakubas et al. 1994, Kay and Wagner 1994, Knight and Wallace 1989, Norland et al. 1996, Renkin et al. 1994, Renkin and Despain 1996a, Romme and Turner 1991, Turner et al. 1994, Turner et al. 1997)(Fig. 10). The majority of papers (79%) discussed coniferous forest with regard to the effects of fire.

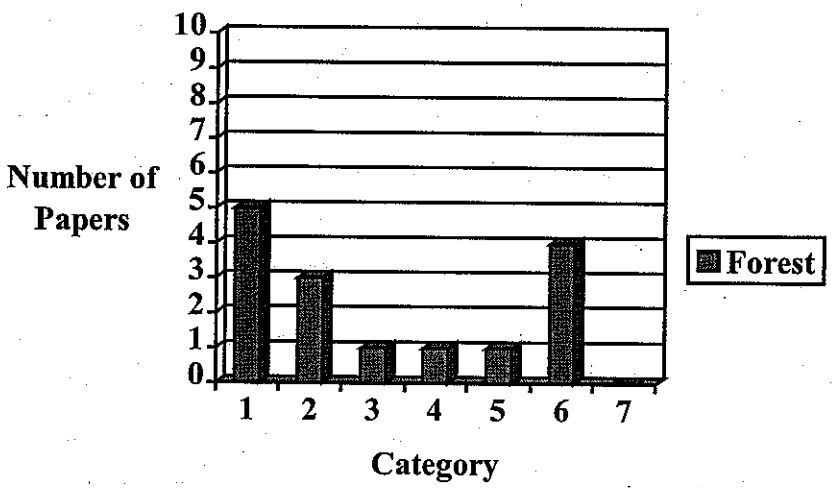
The increase in global temperatures during the past century has been well documented (Watson 2001). Romme and Turner (1991) suggested that if the climate in YNP becomes warmer and precipitation increases, forests would encroach towards lower elevation areas, thereby reducing non-forest habitats and potentially causing increased use of forest habitat by ungulates. However, climatic data collected during the past century indicate that YNP has become more arid and precipitation has declined, thereby increasing the risk of fire (Balling et al. 1992).

Fires in Yellowstone's forests are typically stand-replacing and occur at intervals of 150-300 years or more, with flammability increasing as stands approach maturity (Balling et al. 1992). Approximately 25-30% of YNP was affected in 1988 by canopy fires, which greatly modified forest physiognomy (Knight and Wallace 1989) and provided a unique opportunity for examining the immediate effects and post-fire responses of the park's flora and fauna (Christensen et al. 1988).

Although fire favors serotinous species (Despain et al. 1996), the rate of post-fire plant reestablishment is influenced by the size of burned patch, the distance to the nearest unburned patch, and the amount and spatial distribution of burn severity (Turner et al.1994b). Severe fires may destroy canopy seedbanks, reduce seedling production

(Turner et al.1994b) and increase soil runoff (Farnes 1996). High intensity fires can reduce species richness by suppressing sprouting of forest herbs and aspen while favoring lodgepole pines (Turner et al. 1997). Christensen et al. (1988) suggested that post-fire tree establishment and growth might be poor or absent on sites where soil temperatures were high or the duration of heating was long. In fact, high intensity fires in 1988 caused high mortality of canopy seedbanks (Turner et al. 1994).

Figure 10. Distribution of inferential categories for elk/forest literature.



Ellis et al. (1994) found that lodgepole pine seedling density was higher in moderately burned than severely burned transects and was poorly correlated with cones remaining in the crowns of dominant trees. Ellis et al. (1994) attributed differences in seedling densities between moderately and severely burned transects to differential seed mortality in response to fire intensity. Lodgepole pine seedlings decreased in number with increasing distance to unburned forest, with density and cover of pines greater in smaller burned patches than large ones (Turner et al. 1994). Ellis et al. (1994) further suggested that the serotiny mosaic is related to burn severity in much the same way as seedling densities. Severely burned areas with extremely low initial seedling densities will develop into open stands containing few dominant individuals that slowly fill in canopy gaps and produce a mixed age stand, and that the majority of the park's burned areas will be characterized by extensive evenly-aged forests.

Coniferous forest is an important habitat type for elk in the western United States that provides thermal (Beall 1974) and security cover (Cassier et al. 1992), bedding sites (Marcum 1975) and food (Nelson and Leege 1982). Bedding sites typically have high crown cover and feeding usually occurs in low cover (Marcum 1975), with overstory stand density frequently determining understory herbage productivity (McConnell and Smith 1971).

Although browsing by ungulates may increase post-fire due to increases in forage availability and nutritional content (Knight and Wallace 1989), conifers have relatively little forage value compared to aspen and willow (Nelson and Leege 1982). Post-fire, willow biomass increased (Norland et al. 1996) and burned aspen responded quickly to fire by root sprouting (Knight and Wallace 1989). Elk preferred burned willows that had enhanced forage quality and higher production than those unburned (Norland et al.1996). Although aspen may initially outcompete lodgepole pine following fire, preferential browsing of aspen by ungulates can negate aspen growth and result in dominance by lodgepole pine (Renkin et al. 1994).

Reconciliation of Reviewed Literature and Pathways Linking Forest and Elk Ecology. The following list identifies the major pathways and feedback loops linking forest and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

2° Stressor	→	**Ecological Effects**
Forest		Elk Population Ecology
Forest		Elk Condition
Forest		Elk Foraging

Feedbacks	
Elk Population Ecology	Forest
Elk Condition	Forest
Elk Foraging	Forest

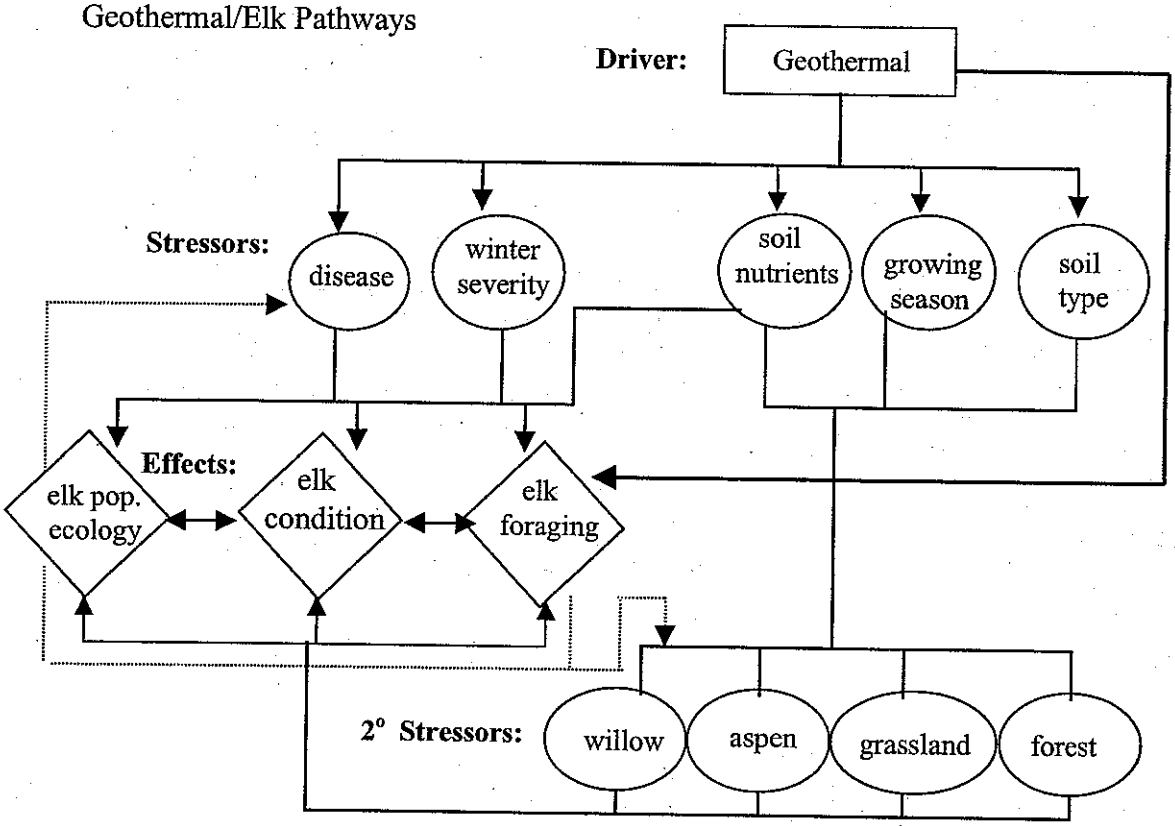
Cassier et al. (1992) addressed the "Forest → Elk Population Ecology" pathway and found increased use of high elevation coniferous forests by elk in response to human disturbance.

Jakubas et al. (1994) addressed the "Forest→ Elk Foraging" pathway to determine whether the 1988 fires improved the overall nutritional quality of lodgepole pine by altering the chemical composition and digestibility of the bark. They found that burned lodgepole pine bark was more digestible and contained more crude protein and less secondary metabolites than that of unburned trees.

Renkin et al. (1994) addressed the "Elk Foraging → Forest" feedback loop and found that post-fire preferential, and repeated browsing of aspen by elk may allow lodgepole pine to outcompete aspen and become the dominant canopy species.

Geothermal/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between geothermal areas and elk on the northern range.

Geothermal/Elk Pathways

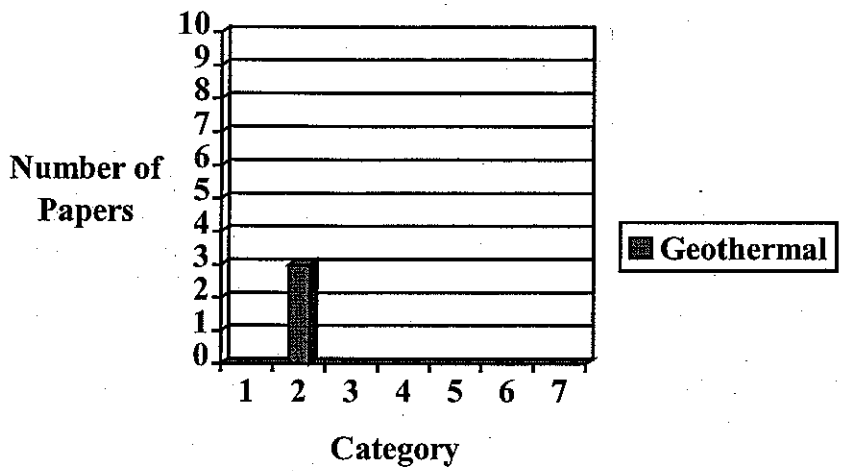


Synopsis of Reviewed Literature. We found 3 papers that addressed geothermal features in YNP and elk relations with other wildlife (Garrott et al. 2002, Green et al. 1997, Tracy and McNaughton 1995) (Fig. 11). Although two papers (Green et al. 1997, Tracy and McNaughton 1995) were placed in category 2, and thus had good inferential power, the references to geothermal activity and elk were indirect and suggestive at best. Conversely, Garrott et al. (2002) was also placed in category 2, but this research directly examined the influence of geothermal phenomena on elk ecology in YNP.

There is no doubt that geothermal features such as Old Faithful are major attractions to human visitors of Yellowstone National Park (Greater Yellowstone Coordinating Committee 1987). Their value to wildlife, however, is equivocal. While a handful of individuals of a variety of species may benefit from steaming vents that serve as buffers to winter temperature and snow accumulation, these same areas are frequented sufficiently by humans that use by wildlife may be diminished (Green et al.1997). Nonetheless, unusually high concentrations of animals in geothermals may promote the transmission of disease among elk, and offset thermal benefits derived from these areas. On the other hand, minerals associated with geothermals that are unavailable in similar concentrations elsewhere may reduce competition among elk (Tracy and McNaughton

1995). In a system such as YNP where forage availability, winter severity, and interspecific competition serve as mechanisms for a density-dependent, natural regulation policy, a firm understanding of elk/geothermal relations appears essential for effective elk management.

Figure 11. Distribution of inferential categories for elk/geothermal literature.



Reconciliation of Reviewed Literature and Pathways Linking Geothermal Areas and Elk Ecology. The following list identifies the major pathways and feedback loops linking geothermal areas and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor**	→	**Ecological Effects**
Geothermal	Disease		Elk Population Ecology
Geothermal	Disease		Elk Condition
Geothermal	Disease		Elk Foraging
Geothermal	Winter Severity		Elk Population Ecology
Geothermal	Winter Severity		Elk Condition
Geothermal	Winter Severity		Elk Foraging
Geothermal	Soil Nutrients		Elk Population Ecology
Geothermal	Soil Nutrients		Elk Condition
Geothermal	Soil Nutrients		Elk Foraging

Driver →	Stressor →	2° Stressor →	Ecological Effects
Geothermal	Growing Season	Willow	Elk Population Ecology
Geothermal	Growing Season	Willow	Elk Condition
Geothermal	Growing Season	Willow	Elk Foraging
Geothermal	Growing Season	Aspen	Elk Population Ecology
Geothermal	Growing Season	Aspen	Elk Condition
Geothermal	Growing Season	Aspen	Elk Foraging
Geothermal	Growing Season	Grassland	Elk Population Ecology
Geothermal	Growing Season	Grassland	Elk Condition
Geothermal	Growing Season	Grassland	Elk Foraging
Geothermal	Growing Season	Forest	Elk Population Ecology
Geothermal	Growing Season	Forest	Elk Condition
Geothermal	Growing Season	Forest	Elk Foraging
Geothermal	Soil nutrients	Willow	Elk Population Ecology
Geothermal	Soil nutrients	Willow	Elk Condition
Geothermal	Soil nutrients	Willow	Elk Foraging
Geothermal	Soil nutrients	Aspen	Elk Population Ecology
Geothermal	Soil nutrients	Aspen	Elk Condition
Geothermal	Soil nutrients	Aspen	Elk Foraging
Geothermal	Soil nutrients	Grassland	Elk Population Ecology
Geothermal	Soil nutrients	Grassland	Elk Condition
Geothermal	Soil nutrients	Grassland	Elk Foraging
Geothermal	Soil nutrients	Forest	Elk Population Ecology
Geothermal	Soil nutrients	Forest	Elk Condition
Geothermal	Soil nutrients	Forest	Elk Foraging
Geothermal	Soil nutrients	Willow	Elk Population Ecology
Geothermal	Soil nutrients	Willow	Elk Condition
Geothermal	Soil nutrients	Willow	Elk Foraging
Geothermal	Soil nutrients	Aspen	Elk Population Ecology
Geothermal	Soil nutrients	Aspen	Elk Condition
Geothermal	Soil nutrients	Aspen	Elk Foraging
Geothermal	Soil nutrients	Grassland	Elk Population Ecology
Geothermal	Soil nutrients	Grassland	Elk Condition
Geothermal	Soil nutrients	Grassland	Elk Foraging
Geothermal	Soil nutrients	Forest	Elk Population Ecology
Geothermal	Soil nutrients	Forest	Elk Condition
Geothermal	Soil nutrients	Forest	Elk Foraging

Feed Backs

Elk Population Ecology	→	Disease
Elk Population Ecology		Willow
Elk Foraging		Willow
Elk Population Ecology		Aspen

Elk Foraging	Aspen
Elk Population Ecology	Grassland
Elk Foraging	Grassland
Elk Population Ecology	Forest
Elk Foraging	Forest

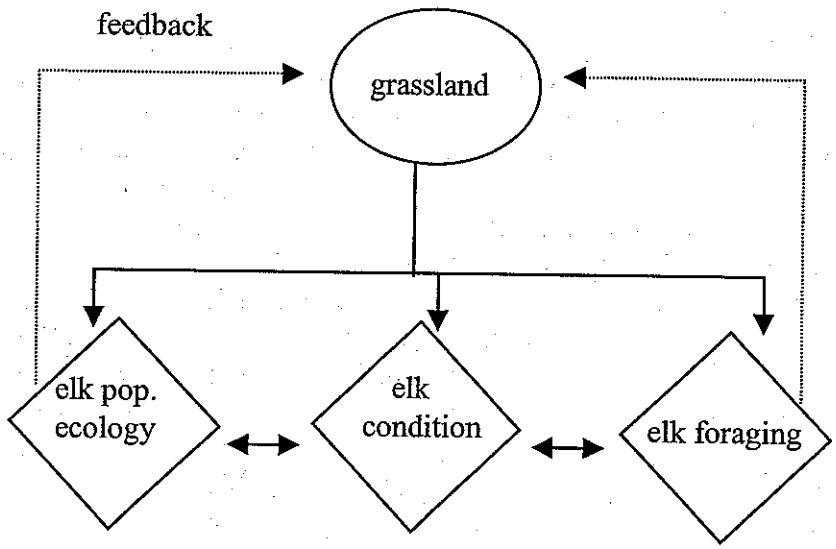
Garrott et al. (2002) addressed the "Geothermal → Soil nutrients → Grassland → Elk Foraging" and "Geothermal → Soil nutrients → Grassland → Elk Condition" pathways. Specifically, the authors contrasted the differences in two YNP locations (Lamar Valley and Madison River Drainage) that differed in geothermal activity. Fluoride and Silica concentrations were elevated in stream water, stream sediment, and plants growing in the geothermally-influenced Madison River Drainage compared with that of Lamar Valley. Elk mandibles collected in the Madison drainage basin contained approximately six-fold higher levels of F than those collected from northern range (Lamar Valley) elk, demonstrating classic signs of fluoride toxicosis. The compromised condition of elk living in the Madison River Drainage is responsible for a dramatically abbreviated survival schedule compared with elk living in Lamar Valley. Because wolves preferentially prey on the young-of-the-year and senescent animals, the geothermally-induced altered age structure of the Madison River elk population results in a higher proportion of the adult population being susceptible to wolf predation.

Green et al. (1997) addressed the "Geothermal → Winter severity → Elk Population Ecology" and "Geothermal → Winter severity → Elk Foraging" pathways, and suggested that elk winter range coincided with geothermal activity.

Tracy and McNaughton (1995) examined the patterns of mineral availability at geothermal sites in YNP ("Geothermal → soil nutrients" pathway) and reported high concentrations of vitamin B and calcium at hydrothermal licks. They suggested that geothermal licks were important mineral sources for ruminants in YNP, and may reduce competition among animals.

Grassland /Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between grasslands and elk on the northern range.

Grassland/Elk Pathways



Synopsis of Reviewed Literature. We found 48 papers and book chapters that addressed grassland issues and elk in YNP (Augustine and McNaughton 1998, Augustine and Frank 2001, Coughenour 1991, Coughenour 1994, Coughenour and Singer 1991, Coughenour et al. 1994, Despain 1996, Frank 1998, Frank and Groffman 1998, Frank and McNaughton 1991, Frank and McNaughton 1992, Frank and McNaughton 1993, Frank and McNaughton 1994, Frank et al. 1994, Frank et al. 1998, Frank et al. 2002, Hobbs 1996, Houston 1976, Houston 1979, Huff and Varley 1999, Knight and Wallace 1989, Merrill et al. 1979, Merrill and Boyce 1991, Merrill and Stanton 1990, Merrill et al. 1994, Norland and Reardon 1996, Norland et al. 1996, Pearson et al. 1995, Peek et al. 1967, Reardon 1996, Romme and Knight 1982, Romme and Turner 1991, Singer 1996b, Singer and Harter 1996, Singer and Renkin 1995, Singer and Mack 1999, Singer and Schoenecker 2003, Singer et al. 1989, Singer et al. 1998, Stohlgren et al. 1999, Tracy and McNaughton 1995, Tracy and McNaughton 1996, Turner et al. 1997, Van Dyke et al. 1994, Van Dyke et al. 1996, Wallace and Macko 1993, Wallace 1996, and Wallace et al. 1995). This well-represented topic includes 31 papers (65%) that were of high inferential power due to their experimental and statistical attributes (category 1; n=20 and category 2; n=11) (Fig. 12).

Grassland ecosystems are globally endangered terrestrial habitats (Frank et al. 1998). Although the temperate grassland biome is well-represented in the United States (Adams et al. 2000) much of it has been drastically reduced and changed by cultivation and domestic livestock (Stoddart et al. 1975, Noss et al. 1995). Some grassland areas in North America have been reduced by >90% since European settlement (Noss et al. 1995, Samson et al. 1998), and today, most exist as remnants of their former vast distribution

(Whitcomb 1987, Noss et al. 1995). Although climate and fire are the most important abiotic factors that maintain grasslands, a suite of herbivores is also important in maintaining characteristic structure and coevolutionary processes (Samson et al. 1998). The uncultivated and relatively undisturbed grasslands of Yellowstone National Park have become laboratories for examining the relations among a variety of grasses, sedges, other herbaceous plants, and the large herbivores that depend upon them. These areas, especially those found in Yellowstone's northern range, are controversial because of the concern over potential overgrazing and because of the boundary issues associated with large, migratory elk herds.

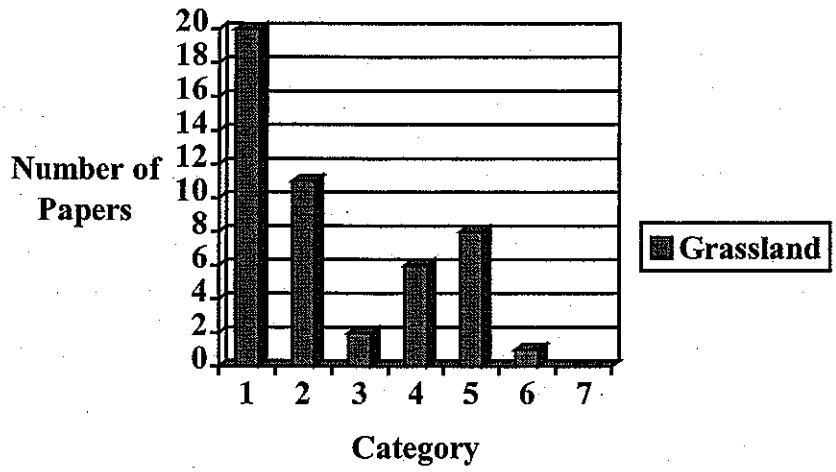


Figure 12. Distribution of inferential categories for elk/grassland literature.

Foraging accounts for a large proportion of elk daily activity (Green and Bear 1990), and elk population size and dispersion is partly influenced by the quality, quantity, and distribution of available forage (Wisdom and Cook 2000). For example, limited forage during winter has been implicated as a factor that causes density-dependent effects in ungulate populations (Merrill and Boyce 1991) and drives seasonal migrations (Adams 1982). The inability to access adequate amounts of forage forces thousands of elk to cross YNP boundaries each year and winter on private lands where forage is more accessible. These seasonal migrations usually result in elk-human conflicts involving property damage and competition with livestock, and disease transmission.

The nutritional quality and spatial distribution of forage results from an interaction between biotic competition and abiotic variability (Wallace et al. 1995). The relationship between forage quality, quantity, and distribution and elk population dynamics and habitat use is further complicated by the positive feedback mechanisms that many plant communities exhibit in response to herbivory and nonrandom deposition of dung and urine (McNaughton 1984, Frank 1998). The spatial distribution of ungulate foraging activities can affect several ecological processes, including nutrient cycling, productivity, succession, and disturbance regimes (e.g., fire) (McNaughton 1984, Coughenour 1991,

Hobbs 1996, Augustine and McNaughton 1998, Frank 1998). Additionally, these influences can be manifested at several temporal and spatial scales depending on various foraging constraints encountered by large herbivores (Senft et al. 1987, Wallace et al. 1995).

Grasses in YNP appear to be fairly resistant to overgrazing because they exhibit compensatory growth, maintain root biomass, and are periodically released from grazing during periods of deep snow when elk migrate to other areas to feed. There does not appear to be any compelling evidence that elk population size in the northern range has exceeded a number sufficient to result in a decline in range quality or an increase in soil erosion. Whereas elk and other grazers certainly impact grazing systems (especially when examined at varying spatial scales), their effects are a part of a suite of biotic and abiotic factors that are difficult to isolate.

The controversy over the potential for elk and other herbivores to overgraze the northern range grasslands is one that likely will be difficult to completely resolve because of the incomplete record of historical conditions in and around YNP. The degree to which conditions have fluctuated over two centuries as the result of human activities, climatic trends and cycles, herbivore abundance patterns (spatial and temporal), and presence or absence of large carnivores is speculative at best. A thorough understanding of the factors that influence the availability and distribution of grasslands, as well as elk foraging strategies, is essential for the effective management of these communities and to ensure that the YNP elk population does not exceed the park's ecological carrying capacity.

Reconciliation of Reviewed Literature and Pathways linking Grassland and Elk Ecology. The following list identifies the major pathways and feedback loops linking grassland and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

2° Stressor	→	**Ecological Effects**
Grassland		Elk Population Ecology
Grassland		Elk Condition
Grassland		Elk Foraging

Feedbacks

Elk Population Ecology	Grassland
Elk Foraging	Grassland

Several authors addressed the "Grassland → Elk Population Ecology" pathway (Despain 1996, Frank 1998, Frank and McNaughton 1992, Frank and McNaughton 1994, Merrill and Boyce 1991, Romme and Knight 1982, Romme and Turner 1991, Singer et al. 1989, and Van Dyke et al. 1994). Romme and Turner (1991) suggested two main climate change scenarios that could affect ungulate population ecology, including a "warm-wet"

scenario that favored forested versus non-forested habitat, and a "warm-dry" scenario that could lead to an increase in grassland range but likely be offset by decreases in quality and quantity of available forage. Elk habitat was found to be more variable at the stand level rather than the watershed level during the past two centuries (Romme and Knight 1982). Several authors found that elk migration and subsequent foraging coincided with peak nutritional output of grasslands (Frank 1998, Frank and McNaughton 1992, Frank and McNaughton 1994), and Despain (1996) suggested that elk migration maybe related to blue bunchgrass flowering. Merrill and Boyce (1991) found that phytomass explained 77% of the variation in elk population growth rates and influenced demographic ratios. In keeping with these findings, Van Dyke et al. (1994) found that elk populations that used higher quality summer range had increased productivity, and Romme and Knight (1982) suggested that elk populations may fluctuate in response to the availability of upland summer habitat. Singer et al. (1989) predicted an increase in elk population following the 1988 fires due to post-fire growth and nutritional enhancement of grasslands.

A number of authors addressed the "Grassland → Elk Foraging" pathway (Norland et al. 1996, Pearson et al. 1995, Singer et al. 1989, Singer and Harter 1996, Tracy and McNaughton 1995, Tracy and McNaughton 1996, Turner et al. 1997, Van Dyke et al. 1994, Van Dyke et al. 1996, and Wallace et al. 1995). Graminoids constitute the majority of elk diet, with selection for species with higher nutrition (Van Dyke et al. 1994). Tracy and McNaughton (1995) suggested that a sodium deficiency in grasses might cause elk to seek this mineral at licks to supplement their diet. Wallace et al. (1995) found that ungulate feeding site selection was based primarily on forage quantity at broad spatial scales. Singer et al. (1989) predicted an increase in the palatability, digestibility, and availability of herbaceous and shrub cover following the 1988 fires in YNP. Further, they forecasted that elk would decrease home ranges in burned areas due to the availability of fire-responsive forage. The 1988 fires shifted large areas of forested habitat towards non-forest communities such as grasslands (Turner et al. 1997). Post-fire, grasses and forbs increased (Van Dyke et al. 1996), with grasses having increased above-ground primary productivity, nitrogen, and phosphorus mineralization (Tracy and McNaughton 1996). Norland et al. (1996), however, found that two-years post-fire, the diversity of herbaceous cover, amount of shrub cover, and forage biomass were unchanged, but the nutritional quality of these habitats had increased. Several studies found that elk preferred burned grasslands to that unburned (Pearson et al. 1995, Singer and Harter 1996, Tracy and McNaughton 1996, Van Dyke et al. 1996).

Coughenour (1994), Frank et al. (1994), Augustine et al. (2001), and Singer and Schoenecker (2003) addressed the "Elk Population Ecology → Grassland" feedback loop. Coughenour (1994) attempted to calculate spatial and temporal patterns of herbivory in YNP by incorporating variations in forage quality, elk nutritional requirements, and snow depth. Frank et al. (1994) found that elk migration and foraging increased nitrogen mineralization in grasslands and that elk excrement accounted for 27% of the annual N mineralized, a contribution greater than that of senescent plant tissue. Net movement of N occurred over the course of the year from high elevation summer range into ungulate biomass that was subsequently lost from animals to winter range

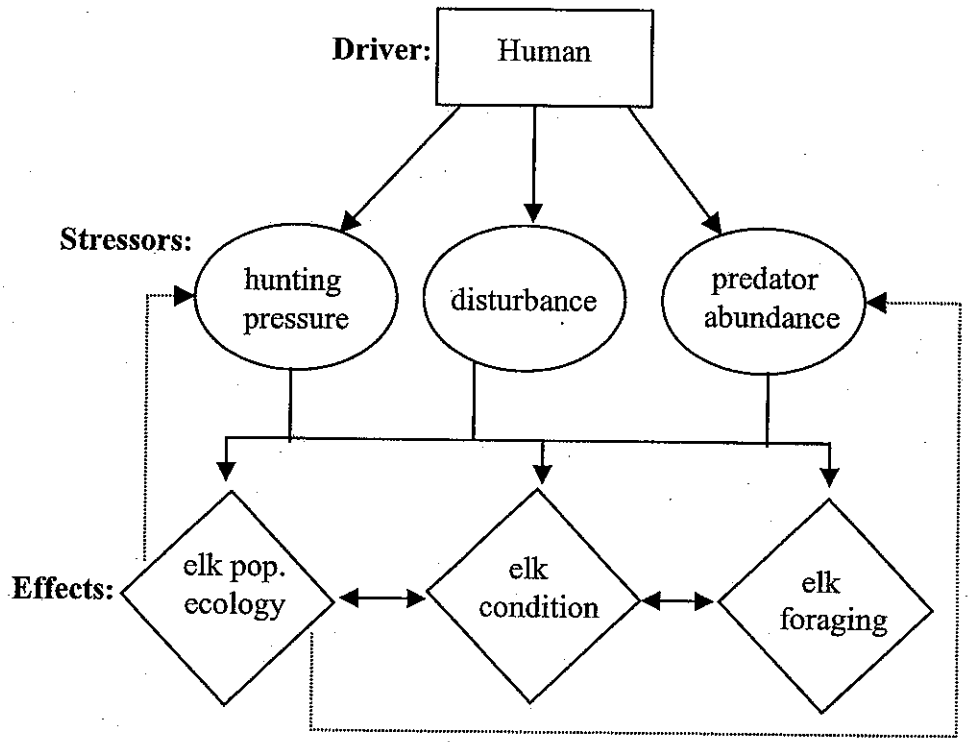
(Frank et al. 1994). Frank et al. (1994) also found that the annual rate of mineralization in YNP was higher than that found in other western grassland systems. Augustine et al. (2001) demonstrated that in addition to the effects of topography and vegetation on spatial patterning of resource availability, biotic components of ecosystems such as large herbivores not only respond to resource heterogeneity, but also play a significant role in generating observed patterns. Their findings show herbivory also modifies soil heterogeneity at small spatial scales, increasing the amount of variability in the soil environment experienced by a plant individual. Singer and Schoenecker (2003) compared the ecosystem effects of ungulate herbivory on nitrogen cycling in two western national parks, Rocky Mountain (RMNP) and YNP. In response to grazing at YNP, grassland plant species abundance was largely unaltered, net annual aboveground primary productivity was stimulated except during drought, consumption of key N-rich forages was moderate and their abundance was sustained, soil N mineralization rates doubled, N pools increased, aboveground N yields increased, and N concentrations increased in most grassland species. In contrast, grazing in grasslands in RMNP resulted in no detectable acceleration or deceleration of nutrient cycling.

Several authors addressed the "Elk Foraging → Grassland" feedback pathway (Coughenour 1991, Frank and Groffman 1998, Frank and McNaughton 1993, Frank and McNaughton 1994, Frank et al. 2002, Merrill et al. 1979, Merrill et al. 1994, Merrill and Stanton 1990, Reardon 1996, Singer 1996b, Singer and Renkin 1995, Stohlgren et al. 1999, Wallace and Macko 1993, and Wallace 1996). Elk grazing was found to stimulate above-ground primary productivity of plants (Frank and McNaughton 1993) and increase nitrogen of above-ground, but not below-ground biomass (Merrill et al. 1979, Merrill et al. 1994). Elk were found to consume 45% of above-ground primary productivity (Frank and McNaughton 1994), although grazing plants were found to recoup biomass losses by the end of the growing season (Merrill et al. 1994). Grazers caused a decrease in soil moisture and increase in nitrogen mineralization (Frank and Groffman 1998). Coughenour (1991) found that winter grazing by elk reduced dead grass and leaf litter and shifted nitrogen from decomposers to grazers. Grazing has been found to cause root hair senescing (Merrill et al. 1994) that increases available substrates for decomposers (Merrill and Stanton 1990) and which stimulates lateral root growth that provides microhabitat for nematodes (Merrill et al. 1979, Merrill et al. 1994). Reardon (1996) found that exclosure of ungulates did not significantly affect vegetative cover. Singer (1996b) concluded that elk herbivory did not influence the species composition of grasses, forbs, and shrubs, but did increase their protein concentration. Wallace (1996) described a negative correlation between plant size and grazing intensity, with small, previously ungrazed plants being preferred by ungulates. Singer and Renkin (1995) found that even though big sagebrush only comprised 8% of elk diet, elk limited the species at low elevations. Although grazed areas have not been found to cause increased species richness (Stohlgren et al. 1999), Wallace and Macko (1993) found that grazing caused a compensatory response in plants in which nitrogen is competitively procured through local uptake, and which leads to increased diversity of grazed plant communities. Frank et al. (2002) examined the effects of large herds of migratory ungulates on ecosystem primary production comparing above ground (NAP) and below ground production (NBP) in grazed and ungrazed (fenced) grassland in nine widely variable grasslands. Their

results indicate that the predominant effect of grazers on grasslands was a facilitating influence on the below ground food web. Additionally, grazer-enhance root mortality provides a mechanistic explanation for herbivores increasing soil organic matter and rates of nutrient turnover in Yellowstone grasslands.

Human/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between humans and elk on the northern range.

Human/Elk Pathways

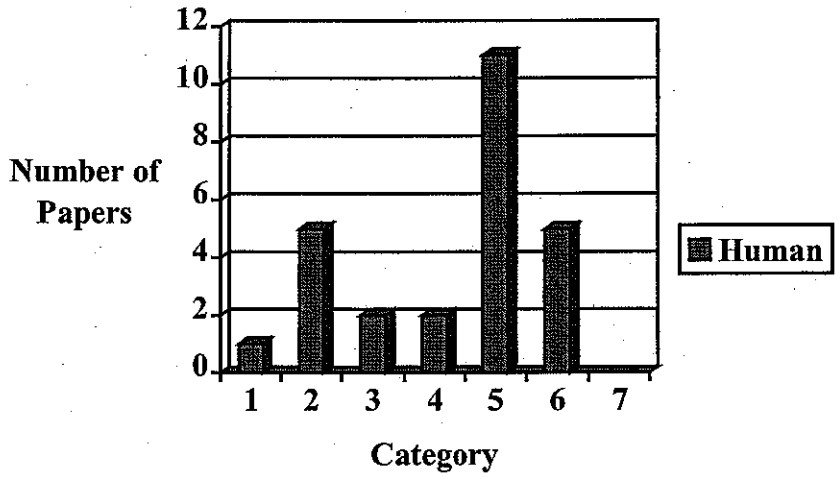


Synopsis of Reviewed Literature. We found 26 papers that addressed direct and indirect human influences on elk in YNP (Boyce 1991, Boyce 1996, Boyce 1998, Cassirer et al. 1992, Chadde and Kay 1991, Cole 1969, Cole 1971, Coughenour and Singer 1991, Coughenour and Singer 1996b, Creel et al. 2002, Houston 1976, Huff and Varley 1999, Kay 1985, Kay 1997, Kay 1998, Kay and Wagner 1994, Kay and Wagner 1996, Lemke et al. 1998, Meagher 1989, Murphy 1998, Singer 1996a, Singer et al. 1998, Thompson and Henderson. 1998, Whitlock et al. 1991, Wright 1998, Yochim 2001). Few of the papers (32%) exhibited inferential or statistical power (Fig. 13). Most (57%) were essays that discussed the relative merit of natural regulation in Yellowstone National Park. Only one paper dealt directly with the impact of human disturbance on elk behavior and winter energy balance (Cassirer at al. 1992). Another study addressed the physiological response of elk and wolves to snowmobile activity (Creel et al. 2002). Three papers examined the need to communicate complex management issues with the public (Meagher 1989, Thompson and Henderson 1998, Wright 1998).

Humans have clearly had tremendous impacts on the global environment (Goudie 2000). As managers become increasingly aware of the dangers of managing national parks as isolated geographic and administrative units, entire volumes have been produced to address a problem that largely involves human activities and perceptions (Wright 1996). It is increasingly clear that Leopold's (1949) vision of parks as museum-like ecological

vignettes is insufficient to protect dwindling biodiversity – trans-border issues and challenges are not only threats to biodiversity issues within parks, but opportunities for enhancing wildlife populations (Harris et al. 1996). Effective communication with and involvement of the public in wildlife management decisions is essential for capitalizing on such opportunities (Siemer at al. 2001).

Figure 13. Distribution of inferential categories for elk/human literature.



Yellowstone National Park represents an immense outdoor laboratory for examining controversial management actions including the impact of human activities and management philosophies on biodiversity and ecological and evolutionary processes. The natural regulation paradigm of YNP has been the focus of case studies for more than 3 decades (Gilbert 1971). The natural regulation debate will likely be a continuing topic of discussion for wildlife managers in the future. There is little need to divert scarce research dollars to this argument. On the other hand, the paucity of studies on public opinion and education opportunities related to elk issues on the northern range is a largely untapped field of applied research. Similarly, we only found 1 papers that examined the influence of human activities outside of YNP on elk herd movements or demography (Lemke et al. 1998). The notion of buffers to human activities may prove to be a particularly important avenue of study at YNP, especially with regard to its large and potentially dangerous large mammals. As Peterson (1996:432) observed, "*Inclusion of the* 'transition zone' *in a broad research program emphasizes the importance of including social, economic, and cultural factors in biological studies...Social elements should be integrated with ecosystem-scale research and management to the greatest extent possible...For example, if scientists are studying how to enhance grizzly bear populations, what will be the impact of increased bear encounters on park visitors? Will the bears impact livestock on adjacent private land? Including local stakeholders during the development of the research program may have the benefit of increased support for the program...and reduced antagonism and litigation. Broad participation in the design and conduct of a research project helps to maintain a focus on the original objectives*

and potential application of the data." It would take little to amend this recommendation into a YNP northern range elk context: the study of and solutions to cross-boundary impacts from within and without the park (brucellosis, depredation, harvest, highway hazards, etc.) should include focused and on-going research to measure and engage public opinion in the process.

Reconciliation of Reviewed Literature and Pathways linking Humans and Elk Ecology. The following list identifies the major pathways and/or feedback loops linking humans and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Driver**
Human	Fire

Driver →	**Stressor**	→	**Ecological Effects**
Human	Hunting Pressure		Elk Population Ecology
Human	Hunting Pressure		Elk Condition
Human	Hunting Pressure		Elk Foraging
Human	Disturbance		Elk Population Ecology
Human	Disturbance		Elk Condition
Human	Disturbance		Elk Foraging
Human	Predator Abundance		Elk Population Ecology
Human	Predator Abundance		Elk Condition
Human	Predator Abundance		Elk Foraging

Feedbacks

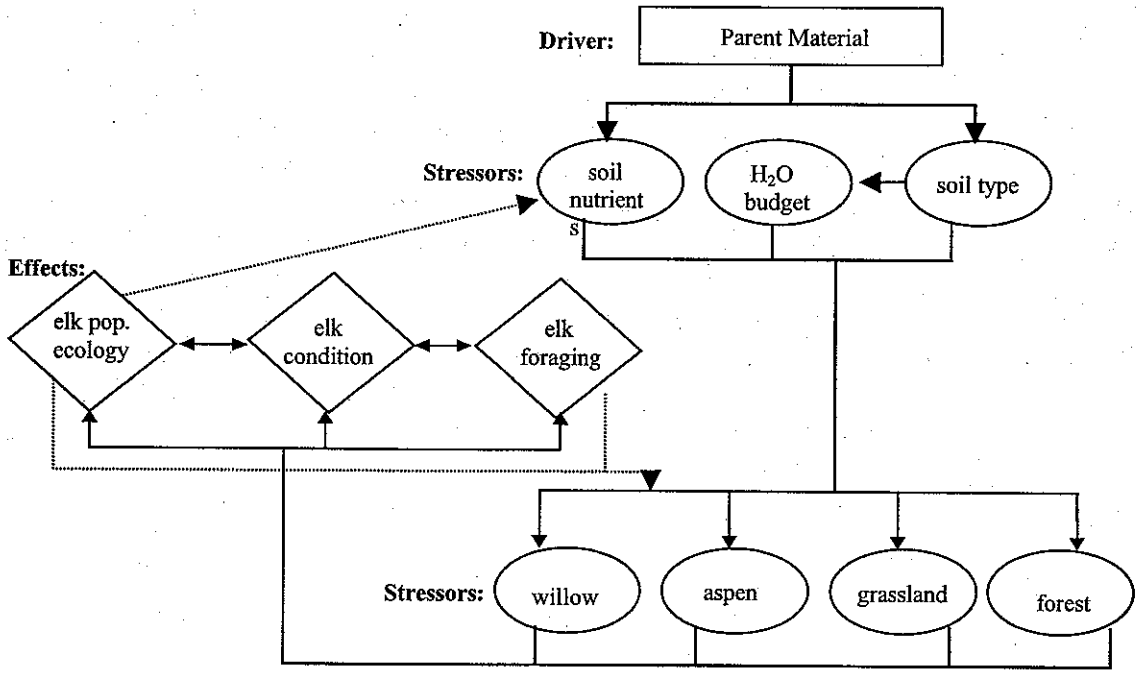
Elk Population Ecology	→	Hunting Pressure
Elk Population Ecology		Predator Abundance

Cassierer et al. (1992) and Creel et al. (2002) addressed the "Human → Disturbance → Elk Condition" pathway. Cassierer et al. (1992) found that elk that fled from disturbance caused by skiers utilized 5.5% of their daily energy budget in doing so. Creel et al. (2002) concluded that although glucocorticoid concentrations of elk were higher in response to snowmobiles than to wheeled vehicles, no evidence was found that current levels of snowmobile activity are affecting the population dynamics of elk at YNP.
Lemke et al. (1998) addressed the "Human → Hunting Pressure → Elk Population Ecology" pathway and found that hunting outside YNP did not limit the park's elk herd or its use of available winter range.

Several authors addressed the "Human → Predator Abundance → Elk Population Ecology" pathway (Chadde and Kay 1991, Kay 1985, Kay and Warner 1996, Murphy 1998, Singer 1996a, Whitlock et al. 1991). Most of these papers dealt with issues concerning the natural regulation management policy. Given that this policy was implemented without the full suite of the park's carnivores, namely wolves, much of the research focus has been on whether an overabundance of ungulates and its associated problems, such as overgrazing, exists. Several authors (Chadde and Kay 1991, Kay 1985, and Kay and Warner 1996) suggested that elk became overabundant since the park's establishment and have subsequently restricted aspen communities. Further, these authors contend that this overabundance signals a failure of the natural regulation policy. Singer (1996a) suggested that the elimination of wolves, human-disrupted elk migrations, and increased elk wintering in YNP have reduced willow abundance. However, based on data collected from lake sediment and pollen, Whitlock et al. (1991) determined that ungulates had not caused soil erosion or reduced plant communities in excess of that found during the past 20,000 years, thus validating support for the natural regulation policy. Murphy (1998) found that the hunting of mountain lions outside of YNP affected the number and age demographics of ungulate prey.

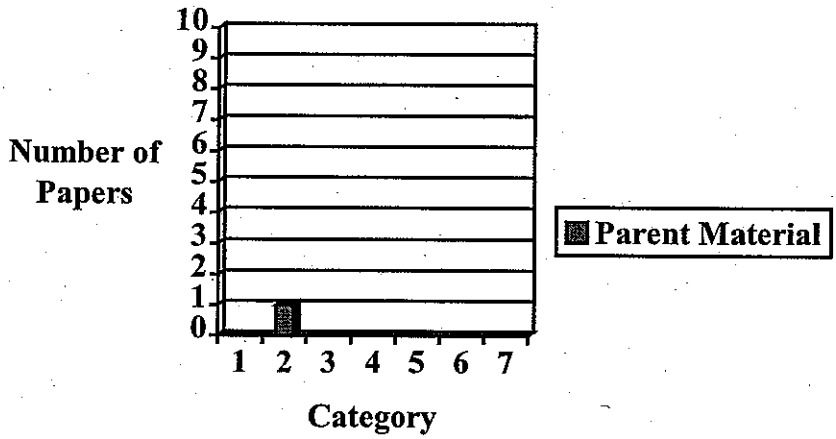
Parent Material/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between parent material and elk on the northern range.

Parent Material/Elk Pathways



Synopsis of Reviewed Literature. We found 1 paper that discussed the influence of parent material on the ecology of northern range ungulates or their habitat (Garrott et al 2002)(Fig.14).

Figure 14. Distribution of inferential categories for elk/ parent material literature.



Reconciliation of Reviewed Literature and Pathways Linking Parent Material and Elk Ecology. The following list identifies the major pathways and/or feedback loops linking parent material and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor →**	**2° Stressor →**	**Ecological Effects**
Parent Material	Soil Nutrients	Willow	Elk Pop. Ecology
Parent Material	Soil Nutrients	Willow	Elk Condition
Parent Material	Soil Nutrients	Willow	Elk Foraging
Parent Material	Soil Nutrients	Aspen	Elk Pop. Ecology
Parent Material	Soil Nutrients	Aspen	Elk Condition
Parent Material	Soil Nutrients	Aspen	Elk Foraging
Parent Material	Soil Nutrients	grassland	Elk Pop. Ecology
Parent Material	Soil Nutrients	grassland	Elk Condition
Parent Material	Soil Nutrients	grassland	Elk Foraging
Parent Material	Soil Nutrients	conifer forest	Elk Pop. Ecology
Parent Material	Soil Nutrients	conifer forest	Elk Condition
Parent Material	Soil Nutrients	conifer forest	Elk Foraging
Parent Material	Soil Type	Willow	Elk Pop. Ecology
Parent Material	Soil Type	Willow	Elk Condition
Parent Material	Soil Type	Willow	Elk Foraging
Parent Material	Soil Type	Aspen	Elk Pop. Ecology
Parent Material	Soil Type	Aspen	Elk Condition
Parent Material	Soil Type	Aspen	Elk Foraging
Parent Material	Soil Type	Grassland	Elk Pop. Ecology
Parent Material	Soil Type	Grassland	Elk Condition
Parent Material	Soil Type	Grassland	Elk Foraging
Parent Material	Soil Type	Conifer Forest	Elk Pop. Ecology
Parent Material	Soil Type	Conifer Forest	Elk Condition
Parent Material	Soil Type	Conifer Forest	Elk Foraging

Feedbacks

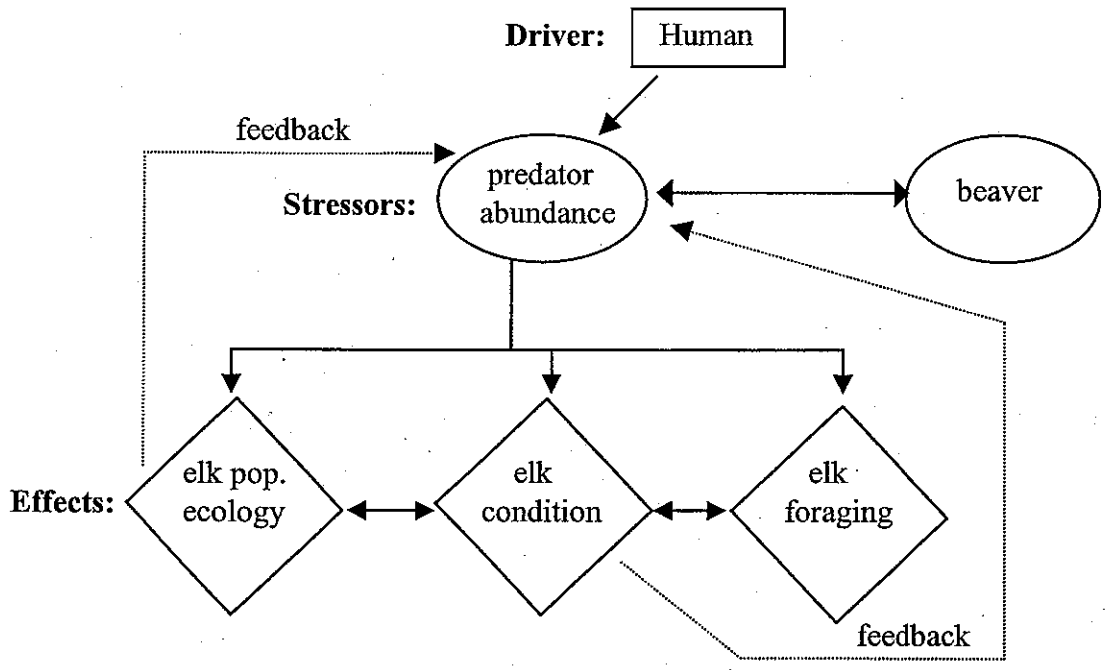
Elk Population Ecology	Soil Nutrients
Elk Foraging	Soil Nutrients

Garrott et al. (2002) addressed the "Geothermal → Soil nutrients → Grassland → Elk Foraging" and "Geothermal → Soil nutrients → Grassland → Elk Condition" pathways. Specifically, the authors contrasted the differences in two YNP locations (Lamar Valley and Madison River Drainage) that differed in geothermal activity. Fluoride and Silica concentrations were elevated in stream water, stream sediment, and plants growing in the

geothermally-influenced Madison River Drainage compared with that of Lamar Valley. Elk mandibles collected in the Madison drainage basin contained approximately six-fold higher levels of F than those collected from northern range (Lamar Valley) elk, demonstrating classic signs of fluoride toxicosis. The compromised condition of elk living in the Madison River Drainage is responsible for a dramatically abbreviated survival schedule compared with elk living in Lamar Valley. Because wolves preferentially prey on the young-of-the-year and senescent animals, the geothermally-induced altered age structure of the Madison River elk population results in a higher proportion of the adult population being susceptible to wolf predation.

Predator/Elk Submodel. The following model depicts the direct and indirect interactions (pathways) that we identified between predators and elk on the northern range.

Predator/Elk Pathways

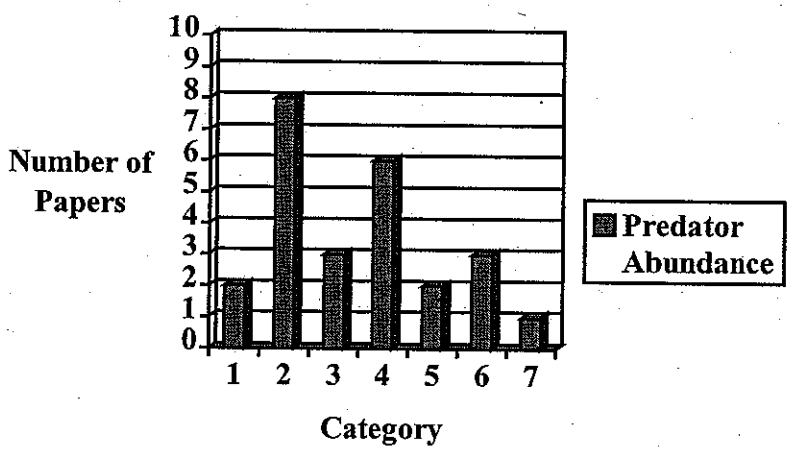


Synopsis of Reviewed Literature. We reviewed 25 papers that examined interactions of elk with predators and/or scavengers in YNP (Boyce 1993, Boyce 1995, Cole 1969, Cole 1972, Crabtree and Sheldon 1999, Fowler and Barmore 1979, French and French 1990, Garrott et al. 2002, Gese 1998, Gese and Grothe 1995, Green et al. 1997, Houston 1978, Houston 1979, Huff and Varley 1999, Kay 1997, Knight et al. 1999, Mattson 1997, Mech et al. 2001, Murphy 1998, Ripple et al. 2001, Romme et al. 1995, Singer 1991, Singer et al. 1997, Singer and Mack 1999, Smith et al. 2000). Half of these studies were descriptive or experimental analyses (categories 1-3)(Fig. 15). Forty percent (n=10) of the papers utilized study designs that allowed mechanistic explanations of elk-predator relations in YNP (categories 1-2). Relations between YNP's wolf and elk populations were covered in several (n=6) papers that were based on predictive models (category 4) and were parts of environmental assessments or other publications relating to wolf reintroduction. Because research on reintroduced wolves is still formative, there is little information with definitive conclusions on wolf-prey relations in YNP. An exception is the finding that naïve ungulate populations learn quickly to modify their behavior in the presence of wild wolves (Berger et al. 2001).

Predation by a carnivore on a single species of large ungulate can have direct effects on the prey population and indirect effects on vegetation via trophic cascades (McLaren and Peterson 1994, Ballard et al. 2001). The absence of the wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) from all or parts of the Greater Yellowstone ecosystem has been implicated in increased herbivory on riparian vegetation and reductions in associated songbird populations (Kay 1985, 1997, Jackson 1993, Berger et al. 2001a, Ripple et al.

2001). Terborgh et al. (1999:58) suggested that "*Our current knowledge about the natural processes that maintain biodiversity suggests a crucial and irreplaceable role of top predators. The absence of top predators appears to lead inexorably to ecosystem simplification accompanied by a rush of extinctions. Therefore, efforts to conserve North American biodiversity in interconnected mega-reserves will have to place a high priority on reestablishing top predators wherever they have been locally extirpated.*"

Figure 15. Distribution of inferential categories for elk/predator literature.



With the return of the wolf and the presence of a resident grizzly bear population, the Greater Yellowstone ecosystem has the potential to serve as a source for an expanding influence of predation on regional ecology and landscape processes. A variety of studies have evaluated the effects of predator removal on deer (*Odocoileus hemionus*) populations (Ballard et al. 2001), however, few studies have examined the effects of predator restoration on prey species (Baker et al. 2001). The restoration of the wolf in YNP should provide an unprecedented opportunity to understand the role of a keystone predator in a system with multiple prey species. In a species-rich predator-prey system such as that found in the Greater Yellowstone ecosystem, such relations will clearly be complex and important to ungulate population dynamics and ecosystem processes (Varley and Brewster 1992). A restored large mammal community includes interrelations between elk and 6 predatory species: wolf, mountain lion (*Felis concolor*), grizzly bear, black bear (*Ursus americanus*), coyote (*Canis latrans*), and human (*Homo sapiens*), as well as several scavengers. Published literature has addressed most of these relations to varying degrees.

Prior to the intensive planning that culminated in wolf reintroductions, research on bears and coyotes dominated the studies of predator-prey relations in Yellowstone National Park (Cole 1972, Crabtree and Sheldon 1999, French and French 1990, Gese 1998, Gese and Grothe 1995, Green et al. 1997, Houston 1978, Knight et al. 1999, Mattson 1997). Many of these observational studies examined in great detail the behavioral components

of such relations and concluded that elk were an important component of the diets of coyote, black bear, and grizzly bear. These carnivores primarily fed on elk carcasses and calves during the spring for a 6-8 week period (French and French 1990, Green et al. 1997, Houston 1978). Predation by these species did not appear to have the potential to reduce elk abundance in the park (Houston 1978). Similarly, mountain lion predation affected a small percentage of the northern range elk population and was not an important factor in population regulation (Murphy 1998, Singer and Mack 1999).

Prior to the reintroduction of wolves, Yellowstone elk populations were controlled by density-dependent mechanisms (Coughenhour and Singer 1996a, Houston 1982, Singer et al. 1997). Harsh winters and competition for food resulted in malnourished animals that either died or were killed by coyotes and bears. Such carnivore-induced mortality was at least partially compensatory, and calves killed by predators in the pre-wolf era were insufficient to limit population growth (Houston 1978, Singer et al. 1997). Predictive models suggested that wolves reintroduced to YNP could reduce elk numbers by 50-91% of ecological carrying capacity (Singer and Mack 1999).

Reconciliation of Reviewed Literature and Pathways Linking Predator and Elk Ecology. The following list identifies the major pathways and feedback loops linking predator and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor →**	**Ecological Effects**
Human	Predator Abundance	Elk Population Ecology
Human	Predator Abundance	Elk Condition
Human	Predator Abundance	Elk Foraging

Stressor →	**Ecological Effects**
Predator Abundance	Elk Population Ecology
Predator Abundance	Elk Condition
Predator Abundance	Elk Foraging

Feedbacks

Elk Population Ecology	Predator Abundance
Elk Condition	Predator Abundance

We reviewed one paper that addressed the "Human → Predator Abundance → Elk Population Ecology" pathway (Murphy 1998). Results from this study supported Ackerman et al.'s (1986) conclusion that altering the sex-age structure of cougar populations (e.g., by hunting) could change the effects of cougars on the numbers and structure of their prey. Ten reviewed papers addressed the "Predator Abundance → Elk Population Ecology" pathway (Boyce 1993, Boyce 1995, Cole 1969, Cole 1972, Crabtree and Sheldon 1999, Fowler and Barmore 1979, Garrott et al. 2002, Houston 1978, Knight et al. 1999, Murphy 1998, Singer et al. 1997). The decline of predators since the 1920's,

especially the eradication of wolves, enabled an increase in the elk population in the Greater Yellowstone Ecosystem (Cole 1969). Before wolf reintroduction, approximately one-third of elk calves died due to predation by grizzly bears, black bears, and coyotes (Singer et al. 1997). However, these same predators in frequently preyed on adult elk (Cole 1972, Crabtree and Sheldon 1999, Knight *et al.* 1999, Murphy 1998). The elk population was thus still thought to be regulated primarily through density dependence (e.g., forage limitations; Singer et al. 1997). Various elk population models suggested that reintroduced wolves will reduce the northern range elk population (Boyce 1993, Boyce 1995, Fowler and Barmore 1979). Now that wolves are once again in the Yellowstone ecosystem, many predictions have been made about the scope and intensity of the effects wolf predation may have on elk populations. A population model developed by Boyce (1993, 1995) predicted that wolves could reduce the northern range elk population by 5-20%, depending on the extent to which wolf predation is compensatory or additive to other mortality sources. Wolf predation may also change the seasonal timing of elk mortality (Houston 1978). Elk mandibles collected in the Madison drainage basin contained approximately six-fold higher levels of F than those collected from northern range (Lamar Valley) elk, demonstrating classic signs of fluoride toxicosis (Garrott et al. 2002). Garrott et al. (2002) concluded that the compromised condition of elk living in the Madison River Drainage is responsible for a dramatically abbreviated survival schedule compared with elk living in Lamar Valley. Because wolves preferentially prey on the young-of-the-year and senescent animals, the geothermally-induced altered age structure of the Madison River elk population results in a higher proportion of the adult population being susceptible to wolf predation.

Ripple et al. (2001) addressed the "Predator Abundance → Elk Foraging" pathway. These authors indicated that elk in YNP appear to be avoiding areas of high wolf-use. Aspen suckers in high wolf-use areas have fewer elk pellet groups and are taller than those in low wolf-use areas (Ripple et al. 2001).

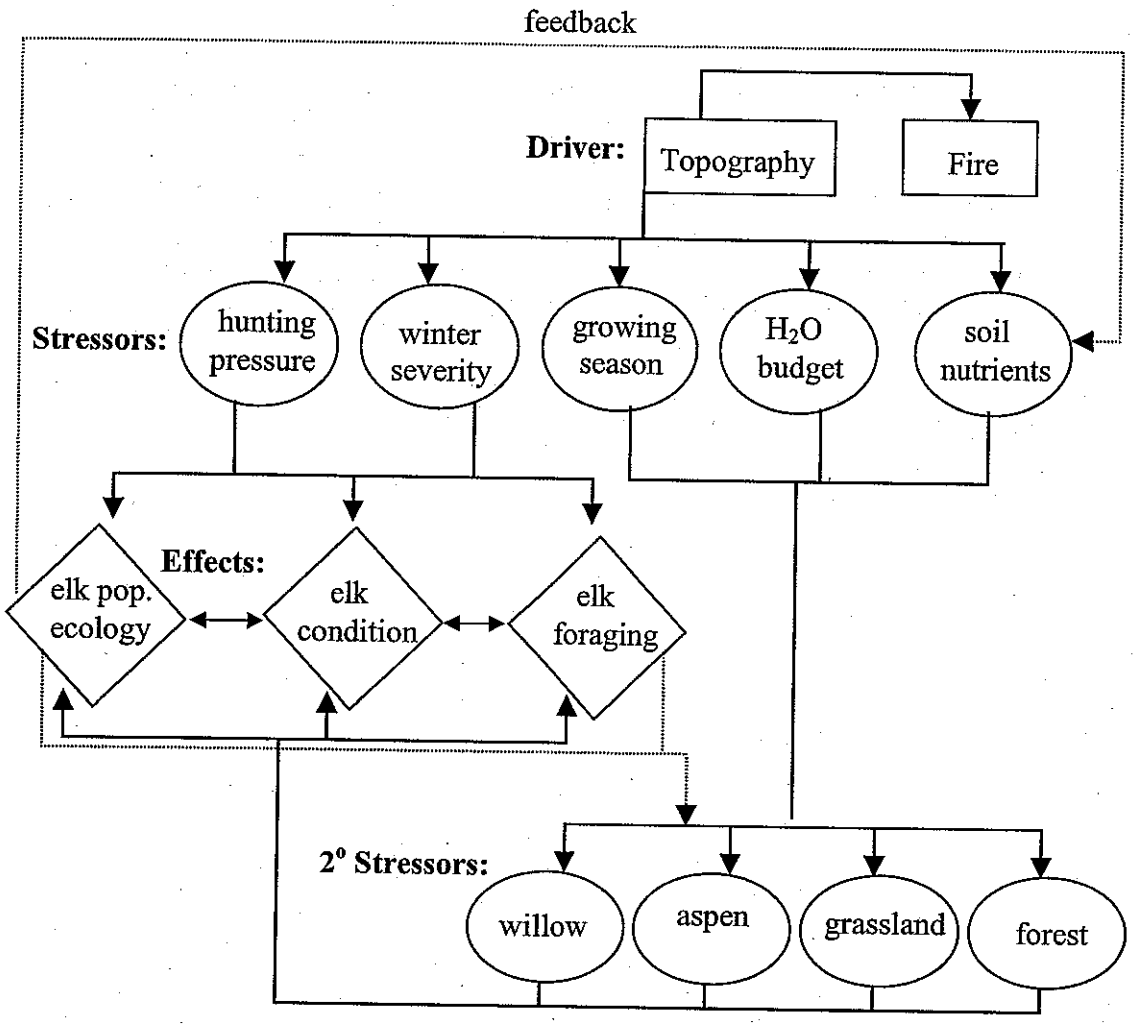
Five reviewed papers addressed the "Elk Population Ecology → Predator Abundance" feedback loop (Green et al. 1997, Houston 1978, Mattson 1997, Singer 1991, Smith et al. 2000). Elk are the preferred prey of wolves in YNP, likely because they are the most abundant ungulate and less risky to kill than bison (Smith et al. 2000). The relatively high density of elk on the northern range in winter provides the best habitat in the park for wolves (Singer 1991). Elk carcasses remain an important springtime food for grizzly bears and other scavengers (Green et al. 1997, Houston 1978). Wolf predation on elk could generate an increase in the number of carcasses available to scavengers (Green et al. 1997). However, grizzly bears are not dependent on elk as a food source. Grizzly predation on elk does not vary with elk herd size, but rather is inversely related to whitebark pine seed production (Mattson 1997). Kay (1997) provided anecdotal evidence suggesting that an overabundant elk population has reduced vegetation forage for grizzly bears, causing grizzlies to leave the park in search of food.

Four reviewed papers addressed the "Elk Condition → Predator Abundance" feedback loop (Farnes 1996b, Garrott et al. 2002, Gese and Grothe 1995, Mech et al. 2001). In severe winters, elk are more vulnerable to predation (Crabtree and Sheldon 1999, Gese

and Grothe 1995, and Mech et al. 2001). As winter progresses, elk condition declines because snow accumulation limits the amount of forage that is accessible to elk (Farnes 1996b, Delguidice et al. 1991). Also, crusted snow hinders mobility for elk, but often can support the weight of coyotes (Gese and Grothe 1995) and wolves (Tefler and Kelsall 1984: Canada). During more severe winters, wolves kill more prey, have a higher killing success rate, and consume less of each carcass (Mech et al. 2001). More elk calves are killed by wolves during milder winters likely because more cows with calves remain in the park, rather than migrating out of the park to areas of lower elevation where fewer wolf packs occur (Mech et al. 2001). Regardless of winter severity, however, Mech et al. (2001) concluded that there will be a substantial number of elk in YNP each winter that are in poor nutritional condition and, consequently, prone to wolf predation. Garrott et al. (2002) concluded that the geothermal-related factors (e.g., fluoride toxicosis) adversely affect the condition of elk living in the Madison River Drainage, and are responsible for a dramatically abbreviated survival schedule compared with elk living in Lamar Valley. The altered age structure of the Madison River elk population results in a higher proportion of the adult population being susceptible to wolf predation

Topography/Elk SubModel. The following model depicts the direct and indirect interactions (pathways) that we identified between topography and elk on the northern range.

Topography/Elk Pathways

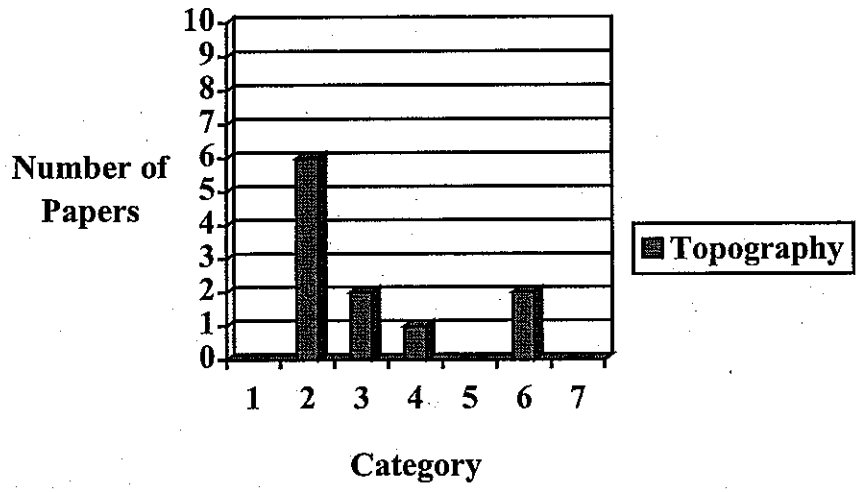


Synopsis of Reviewed Literature. We found 11 papers that addressed relationships between topography and elk or elk habitat (Cassirer et al. 1992, Chadde and Kay 1991, Frank and McNaughton 1992, Frank and McNaughton 1993, Frank et al. 1994, Huff and Varley 1999, Mech et al. 2001, Pearson et al. 1995, Romme and Turner 1991, Shovic 1994, Singer and Renkin 1995). The category most represented (n=6) involved studies that utilized a descriptive/observational approach with a priori sampling design, and provided mechanistic explanations (Category 2)(Fig. 17). Two studies also utilized a descriptive/ observational approach with a priori sampling designs, but did not report any mechanistic explanations (Category 3). The remaining papers were either modeling exercises or observational natural history.

The reviewed papers covered a breadth of research topics. These included 1) the effects of topography on elk habitats (willow, grasslands, and sagebrush); 2) elk foraging

dynamics; 3) elk disturbance by humans; 4) grassland dynamics and nutrient flow; 5) predation; 6) influence on erosion patterns and plant community productivity; and 7) potential influence of climate-related changes in vegetation. The first four topics were investigated most rigorously via research methodologies with a high degree of inferential power (Categories 1, 2, and 3).

Figure 17. Distribution of inferential categories for elk/topography literature.



For decades, wildlife biologists have recognized the importance of topography to elk ecology. Elk utilize topography to avoid predators, human disturbance, severe weather, and for accessing temporarily available forage (Cassier et al. 1992, Skovlin 1982, Wisdom and Cook 2000). Topographic features important to elk behavior and distribution include elevation, slope, and aspect (Skovlin 1982). As a result, effective management of elk and their habitats must take into account potentially confounding topographic influences (Shovic 1994) on elk distribution, behavior, and impacts on plant communities. Wright et al. (1933) noted that elk required upper forest edge for summer range, higher forested slopes for nocturnal cover, and mid-slopes and valleys for winter range. Because elevation interacts with other biological factors to determine vegetation distribution and phenology, it is one of the most important topographic influences on elk ecology (Skovlin 1982). Elevational-influences are generally temporal through the combined effects of growing season length and forage accessibility (Frank and McNaughton 1992, Houston 1976, Huff and Varley 1999, Pearson et al. 1995, Singer and Renkin 1995). Frank and McNaughton (1993) found that the migration of elk in Yellowstone was influenced by the phenology of spring green-up along an elevational gradient.

Reconciliation of Reviewed Literature and Pathways Linking Topography and Elk Ecology. The following list identifies the major pathways and feedback loops linking topography and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4.

Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

Driver →	**Stressor →**	**Ecological Effects**
Topography	Hunting Pressure	Elk Condition
Topography	Hunting Pressure	Elk Population Ecology
Topography	Hunting Pressure	Elk Foraging
Topography	Winter Severity	Elk Population Ecology
Topography	Winter Severity	Elk Condition
Topography	Winter Severity	Elk Foraging
Topography	Growing Season	Aspen

Driver →	**Stressor →**	**2 Stressor →**	**Effect**
Topography	Growing Season	Willow	Elk Population Ecology
Topography	Growing Season	Willow	Elk Condition
Topography	Growing Season	Willow	Elk Foraging
Topography	Growing Season	Aspen	Elk Population Ecology
Topography	Growing Season	Aspen	Elk Condition
Topography	Growing Season	Aspen	Elk Foraging
Topography	Growing Season	Grassland	Elk Population Ecology
Topography	Growing Season	Grassland	Elk Condition
Topography	Growing Season	Grassland	Elk Foraging
Topography	Growing Season	Conifer Forest	Elk Population Ecology
Topography	Growing Season	Conifer Forest	Elk Condition
Topography	Growing Season	Conifer Forest	Elk Foraging
Topography	Water Budget	Willow	Elk Population Ecology
Topography	Water Budget	Willow	Elk Condition
Topography	Water Budget	Willow	Elk Foraging
Topography	Water Budget	Aspen	Elk Population Ecology
Topography	Water Budget	Aspen	Elk Condition
Topography	Water Budget	Aspen	Elk Foraging
Topography	Water Budget	Grassland	Elk Population Ecology
Topography	Water Budget	Grassland	Elk Condition
Topography	Water Budget	Grassland	Elk Foraging
Topography	Water Budget	Conifer Forest	Elk Population Ecology
Topography	Water Budget	Conifer Forest	Elk Condition
Topography	Water Budget	Conifer Forest	Elk Foraging
Topography	Soil Nutrients	Willow	Elk Population Ecology
Topography	Soil Nutrients	Willow	Elk Condition
Topography	Soil Nutrients	Willow	Elk Foraging

Topography	Soil Nutrients	Aspen	Elk Population Ecology
Topography	Soil Nutrients	Aspen	Elk Condition
Topography	Soil Nutrients	Aspen	Elk Foraging
Topography	Soil Nutrients	Grassland	Elk Population Ecology
Topography	Soil Nutrients	Grassland	Elk Condition
Topography	Soil Nutrients	Grassland	Elk Foraging
Topography	Soil Nutrients	Conifer Forest	Elk Population Ecology
Topography	Soil Nutrients	Conifer Forest	Elk Condition
Topography	Soil Nutrients	Conifer Forest	Elk Foraging

Feedbacks

Elk Population Ecology →	Willow
Elk Foraging	Willow
Elk Population Ecology	Aspen
Elk Foraging	Aspen
Elk PopulationEcology	Grassland
Elk Foraging	Grassland
Elk Population Ecology	Conifer Forest
Elk Foraging	Conifer Forest

Several authors (Frank and McNaughton 1992, Frank and McNaughton 1993, Pearson et al. 1995, Singer and Renkin 1995) addressed the "Topography → Growing Season → Grassland → Elk Population Ecology" and the "Topography → Growing Season → Grassland → Elk Foraging" pathways. Elk responded opportunistically to changing forage availability across topographical gradients (Frank and McNaughton 1992, 1993, Singer and Renkin 1995) and altered specific plant communities, such as big sagebrush Singer and Renkin 1995). Ungulates prolonged a nutritionally rich diet by following the wave of plant growth up elevational gradients thereby maintaining a high foraging efficiency (Frank and McNaughton 1992). Topography was found to be a good predictor of grazing activity, with ungulate grazing greatest on low-elevation drier sites across the northern range and on steep south facing slopes (Pearson et al. 1995).

Chaddie and Kay (1991) addressed the "Elk foraging → Willow" feedback loop and found that willow communities at higher elevations with greater snow depth are less affected by ungulate browsing than those at lower elevations with less snow accumulation.

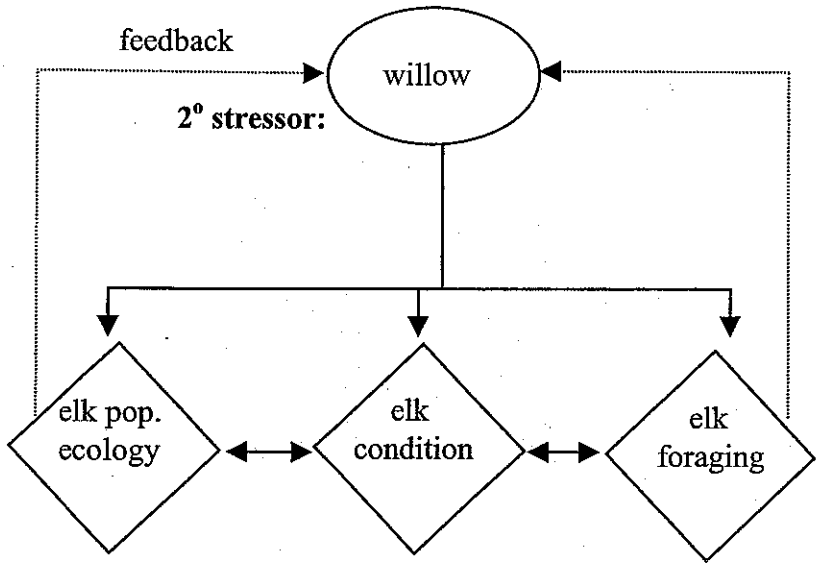
Frank et al. (1994) addressed the "Topography → Soil nutrients → Grassland" pathway" and found that grassland bench sites had higher soil N and C levels than ridgetop and slope sites. High mineralization rates during spring were coincident with intense grazing before ungulates migrated to higher elevations. Further, they suggested that there was a net movement of N over the year from high elevation summer range where ungulates gain body mass, to winter range where body mass is lost.

Frank and McNaughton (1993) addressed the "Elk foraging → Grassland" feedback loop and found that ungulates stimulated primary productivity as they foraged across topographical gradients.

Mech et al. (2001) addressed the " Topography → Winter Severity → Elk Population Ecology" and the "Topography → Winter Severity → Elk Foraging" pathways and found that increased winter severity and snow depth caused elk to seek forage at lower elevations which were occupied by wolf packs, resulting in increased mortality of elk calves.

Willow/Elk Submodel. The following model depicts the direct and indirect interactions (pathways) that we identified between willow and elk on the northern range.

Willow/Elk Pathways

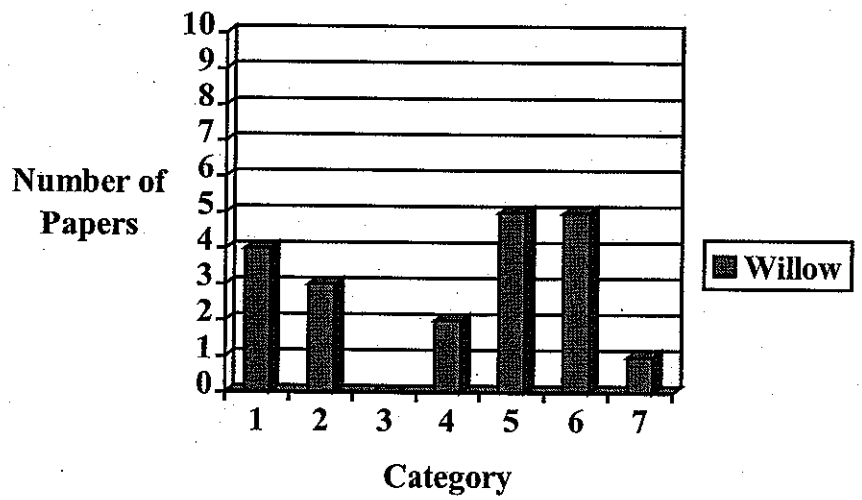


Synopsis of Reviewed Literature. We found 20 papers and book chapters that addressed willow/elk interactions, abiotic influences on willow, and other influences on willow productivity and distribution (Chadde and Kay 1991, Coughenour and Singer 1996b, Houston 1976, Huff and Varley 1999, Jackson 1993, Kay 1985, Kay and Chadde 1991, Kay 1997, Kay and Wagner 1994, Knight 1996, Norland et al. 1996, Singer 1996a, Singer et al. 1994, Singer and Gates 1995, Singer et al. 1998, Singer et al. 1998b, Singer and Mark 1999, Singer and Schoenecker 2003, Wagner et al. 1995, Whitlock et al. 1991). The categories with the greatest representation included those papers that contained a synthetic overview of existing literature that offered a conceptual framework within which to examine temporal or spatial phenomena (category 5), and papers based on observational natural history (category 6) (Fig. 18). Four papers were categorized with high inferential power due to the use of experimental design. Most (55%) of the papers were categorized as a 5 or higher (limited to no inferential power). Seven papers offered mechanistic explanations for changes in appearance and distribution of willow, but no consensus emerged among these papers.

The topic of impacts of elk herbivory on willow is primarily a by-product of the debate on "natural regulation." The literature is quite clear, however, that an interaction of factors explains patterns of willow stature and distribution in Yellowstone's northern range, and that willow population dynamics are as variable as the factors that have been suggested to affect them (Houston 1976, Knight 1996, Norland et al. 1996, Singer 1996a, Singer et al. 1994, Singer and Cates 1995, Singer et al. 1998b, Wagner et al. 1995). It appears as though the real argument is not whether elk may be impacting willows and other tree species, but rather, whether or not the "natural regulation" policy in

Yellowstone National Park is working (Charles and Kay 1991, Houston 1976, Huff and Varley 1999, Kay 1997, Kay and Wagner 1994, Singer et al. 1998, Whitlock et al. 1991).

Figure 18. Distribution of inferential categories for elk/willow literature.



This is likely a debate that may never be satisfactorily resolved because the decision to implement "natural regulation" management is value-laden, and our ability to accurately characterize the historical ecology of the Greater Yellowstone ecosystem is handicapped by time, incomplete records, vague anecdotal descriptions, and fading photographs. Whereas the archival photographs of vegetation offer compelling comparisons of individual sites (Kay and Wagner 1994), they cannot be viewed in the context of the condition of unseen areas that are adjacent to these scenes or to the region at large. More compelling are comparisons of areas inside and outside of exclosures that graphically illustrate the physical appearance of willows that are freed from ungulate browsing (Chadde and Kay 1991, Kay and Chadde 1991). The weakness of such comparisons is that we do not know the identity of the purported browser, and not all browsers are ungulates.

Reconciliation of Reviewed Literature and Pathways linking Willow and Elk Ecology. The following list identifies the major pathways and feedback loops linking willow and elk ecology on the northern range of YNP. Shaded pathways or pathway segments were addressed in reviewed papers that we placed in categories 1 through 4. Pathways or pathway segments that are not shaded were either not addressed in the reviewed literature or were only discussed in papers we placed in categories 5 through 7.

2° Stressor	→	**Ecological Effects**
Willow		Elk Population Ecology
Willow		Elk Condition
Willow		Elk Foraging

Feedbacks →

Elk Population Ecology	Willow
Elk Condition	Willow
Elk Foraging	Willow

Chadde and Kay (1991), Kay and Chadde (1991), Norland et al. 1996, Singer (1996a), Singer et al. (1994), Singer et al. (1998b), Wagner et al. (1995), and Whitlock et al. (1991) address the "Elk Foraging → Willow" feedback loop. While some contend that willow are overgrazed and growth-limited by elk (Chadde and Kay 1991, Kay and Chadde 1991, Wagner et al. 1995), others suggest that additional factors, such as climate, act synergistically with elk browsing to suppress willow in YNP (Singer et al. 1996a, Singer et al. 1994, Singer et al. 1998b). Drought or herbivore-mediated reductions in potential defensive metabolites or increases in primary nutrients in willows increased palatability of willows to ungulates and subsequent suppression of willows (Singer et al 1994). Ungulate herbivory increased on burned willows to such an extent that all burned willows were shorter three years post-fire than were unburned willows (Norland et al. 1996). Still others validate the success of the natural regulation policy in YNP, pointing out the paucity of evidence for ungulate overbrowsing (Whitlock et al. 1991).

Singer et al. (1998b) and Singer and Schoenecker (2003) addressed the "Elk Population Ecology → Willow" pathway. Singer et al. (1998b) found that elk numbers are negatively correlated to annual growth of willows in YNP. Additionally, Coughenour and Singer (1996b) suggested that the YNP elk population was limited by the availability of herbaceous forage rather than willow or aspen. Singer and Schoenecker (2003) compared the ecosystem effects of ungulate herbivory on nitrogen cycling in Rocky Mountain National Park and YNP. They found that effects in short-willow and -aspen vegetation types fit the decelerating nutrient cycling scenario. Willow and aspen showed decreases in soil N mineralization rates, aboveground production, N pools and aboveground N.

SUMMARY OF RESEARCH GAPS AND INFORMATION NEEDS

Aspen Submodel. Although the relative unimportance of aspen as a component of elk forage has been suggested (Coughenour and Singer 1996a, Singer and Norland 1994), browsing by elk may limit growth and maturation of aspen to tree-size in YNP (Kay 1998, Kay and Wagner 1994). The question as to whether aspen distribution and abundance is regulated by elk because it is a preferred food item or whether aspen would comprise a greater proportion of elk diet if it occurred at greater abundances in YNP has yet to be addressed beyond inferences based on incomplete historical documents. The relationship between the amount of aspen in elk diets and elk condition should be examined in order to gain insight as to the relative importance of aspen to elk population ecology on the northern range. Further, an analysis of the relative use of aspen sprouts by smaller herbivores and their role in limiting aspen growth and abundance needs to be examined. Future research on aspen-herbivore relations should continue examining the trophic cascades that may have returned to YNP as the result of re-established wolf populations. The relation between the distribution of wolf packs, wolf activity centers, elk behavior, elk spatial distribution and abundance, aspen seedling establishment, and the release of aspen from herbivory are the ingredients of classic long-term ecological research that may have significant management implications. In addition, research is needed to relate aspen abundance, distribution, and stature to other environmental factors, such as climate and fire, which may operate synergistically with herbivory to affect aspen ecology on the northern range.

Beaver Submodel. The rarity of beaver within the northern range limits research opportunities that might explicate the species' role in the ecosystem. Nonetheless, future research should utilize an approach that provides a mechanistic explanation of beaver influence on northern range ecology, as well as interspecific competition between elk and beaver. Because beaver are rare, researchers will likely need creative study designs that mimic the keystone effects of beaver on the landscape. One such study, utilizing simulated beaver dams and ungulate exclosures is currently underway by Singer and colleagues. We suggest that park managers review the preliminary findings of this study before attempting future research on beaver/elk relationships. Managers and researchers should also review the results of previous work on this subject that may have been conducted outside of the GYE. Such information will likely provide insight into elk/beaver dynamics, as well as existing methodologies that may be applicable to future studies conducted inside the park.

Climate Submodel. Biotic communities at YNP are the products of the over-arching influences of climate – conditions that have gradually changed over millennia. The long time scales over which climatic conditions evolve makes the study of such phenomena difficult because they can easily span many human lifetimes. Nonetheless, the predictive value of routinely and systematically collected weather, hydrology, and soil data increases with the time invested. Thus, we recommend that monitoring programs related to climate and climate change continue or expand as necessary to provide increased predictive capability and to serve as a foundation against which to examine changes in plant and animal distribution and abundance in YNP. Other avenues of research on this

subject could include the effect of precipitation on summer calf recruitment and access to summer range, effects of snow depth on elk forage and distribution, and the effect of early versus late severe winter conditions on elk condition and elk forage. An understanding of these relatively instantaneous responses to annual variation in weather could provide the foundation for predicting the long-term influence of climatic trends on elk and their habitat in the northern range and elsewhere.

Competition Submodel. Despite the presence of seven potential competitors in the park, few studies have empirically examined intra- and interspecific resource and parasite-mediated competition among ungulates. A thorough understanding of niche relationships among Yellowstone ungulates will be essential for their effective management. Such work may also provide empirical evidence regarding the relative merits of natural regulation policy. Additionally, studies that examine competition and niche relationships among Yellowstone's ungulates may also provide insight into potential dependencies and coevolution among species. For example, the decline of the swamp deer (Cervus duvuaceli) was linked to the extinction of the Indian elephant (Elephas maxima) and Indian rhinoceroses (Rhinoceros unicornis) (Gordon 1991). The loss of these bulk feeders from the landscape resulted in the growth and accumulation of coarse grasses that limited swamp deer access to preferred forage. Could a similar relationship exist between bison and a declining northern range pronghorn population? Singer and Norland (1994) suggested that total ungulate numbers could increase nearly 3 fold in the northern range without any evidence of competition because: 1) several of the ungulate species compared were not at ecological carrying capacity when the study was conducted, and therefore competition may not have been intense enough to provide empirical evidence of its occurrence; 2) mild winters during period 2 of the study may have temporarily reduced any detectable resource competition; 3) resource partitioning among northern range ungulates might have occurred at a finer-scale than sampled; and 4) winter range expansion by elk and bison may have increased the ecological carrying capacity for both species, and delayed the observation of niche overlap. Additionally, Tracy and McNaughton (1995) suggested that hydrothermal licks may be important mineral sources for ruminants in YNP, and reduce competition. We recommend a long-term study (>10 years) that utilizes an experimental design that allows researchers to identify fine-scale relationships that exist among ungulate species. Furthermore, a long-term study will help alleviate constraints that environmental and demographic variation imposes on short-term studies.

Disease Submodel. Given the controversial and potentially negative influences of brucellosis on ungulate management and population dynamics in YNP, there has been remarkably little research conducted on this subject. Without an effective vaccine against this introduced disease, management appears destined to include some level of culling, especially with respect to bison. Future efforts should target the development of more effective vaccines and delivery systems, as well as husbandry techniques that reduce infection rates and conflict with owners of nearby domestic herds. Although the incidence of infection is low, there is a large population of elk on the northern range; therefore elk are a threat to cattle as well as bison. Given the recent emphasis on development of a brucellosis vaccine for bison, and that elk are highly gregarious and are

known to habituate to human environments, research is needed to determine the relative transmissibility of brucellosis between bison and elk. CWD has become the preeminent disease concern associated with ungulates in recent years having both increased in frequency and distribution (Williams et al. 2002). Although knowledge about CWD has increased in the last decade, epidemiological and pathogenic mechanisms are not yet fully understood nor have they satisfied public health concerns, thus making management of this disease both difficult and costly. Although CWD has not been detected in the GYE, its potential to dramatically alter elk population dynamics, affect trophic cascades and associated ecological processes, as well as the likelihood that human health concerns could erode recreational use of elk both inside and outside of the park, dictates that CWD surveillance and outbreak protocols be developed within the GYE. Although, Worley (1979) suggested that only one of 27 parasites significantly contributed to elk mortality, it is unclear as to the role these parasites may have in increasing elk susceptibility to predation by reintroduced wolves. Additionally, as elk herd dynamics change in response to increasing wolf predation, research should examine concomitant changes in the prevalence and transmission of brucellosis and other diseases.

Fire Submodel. Perhaps the most important issue in Yellowstone during the next century will be determining how climate change affects the park's ecosystems. Balling et al. (1992) suggested that YNP was becoming increasingly favorable for more frequent fires and greater grassland:forest ratios. Subsequently, elk and other ungulates might spend more time grazing and less time browsing in response to the increased availability of grasses. We suggest congruent monitoring of climate and vegetation patterns to determine the potential for increased fire frequency and its effects on ungulate population ecology and foraging. Past research has illuminated some of fire's direct effects on willow, aspen, and lodgepole pine in YNP. Nonetheless, there is a paucity of information on fire's relation to soil nutrients and subsequent growth mechanisms in important forage species. We suggest controlled experiments be conducted that assess the effect of fire on the structure, nutrients, and microflora of Yellowstone's soils. Such experiments should utilize study designs that provide insight into how fire size, frequency, and intensity influence soil properties and the subsequent responses of various plant communities. Further, we suggest molecular and cellular approaches be used to examine important elk forage species in YNP and the effects of fire on nutrient uptake, growth factors, and other metabolites that are important in anabolic processes. Research has been equivocal as to whether burned areas are preferred by elk over unburned areas in YNP (Norland et al. 1996, Pearson et al. 1995, Singer and Harter 1996, Tracy and McNaughton 1996). We recommend a series of experimental burns in a variety of vegetation types to clarify this issue with respect to habitat-specific preferences of elk. Further, to assess "Fire → Plant Species → Elk Condition" pathways, we suggest that models be developed to examine the energetic cost-benefits for elk with respect to fire heterogeneity, and also which consider fire attributes such as spatial patterns and burn severity, as well as patch plant species composition and associated nutritional values. Hobbs (1996) suggested that the spatial distribution of elk and the subsequent effects of herbivory affect the volatility and fuel load of local plant communities. The potential impacts of elk herbivory in increasing local fire susceptibility via selective browsing, reduction of biomass, and trampling, has yet to be assessed. We recommend a study that investigates relations among ungulate

herbivory, habitat use, and fire occurrence. Finally, we concur with Turner et al. (1997) that research should continue to examine succession on areas burned during the 1988 fires. This will provide managers with a better understanding of potential changes in future elk habitat availability and the possible responses of the GYE elk population to these changes. Additionally, such work may improve our ability to predict future landscape structure under altered fire regimes resulting from climate change.

Forest Submodel. If current climate trends continue (Balling et al. 1992), coniferous forest may become more prevalent, and interior/edge ratios could increase and displace more preferred elk habitat, such as grasslands. Long-term research will be needed that assesses the effects of climate on vegetation patterns and subsequent effects on ungulates in YNP. Concurrent with climate research should be an evaluation that determines potential changes in ungulate foraging patterns. Because conifers are not preferred elk food, the question arises as to whether species such as lodgepole pine will be more frequently consumed in response to their increased availability and expected decrease in preferred elk forage. Will elk and climate work synergistically to create a positive feedback system that further increases conifers and decreases species such as aspen? Such a climate-induced feedback loop could have profound implications for ungulates in YNP, and perhaps lead to declines in ungulate populations and/or migration to seek better foraging grounds outside YNP. Further, how might predator-prey dynamics shift as optimal foraging patches for ungulates decrease, leading to higher concentrations of prey in fewer patches?

Geothermal Submodel. Only two papers in our literature review suggested relations between elk and geothermal areas or processes, and which addressed only 5 of 50 conceived pathways of the submodel. While many pathways remain unexamined, studies that address (1) the influence of geothermal activity in mitigating winter severity and its effect on the growing season and nutrition of important elk forage, and (2) that examine the spatial relationship between elk, humans, and geothermal sites in the northern range of YNP, would facilitate our understanding of elk-geothermal interrelations. If elk are found to preferentially use geothermal areas, investigations into concurrent use of these areas by predators could provide insight into the ecological cost-benefits for elk in these areas. Finally, if elk and other ungulates utilize hydrothermal licks as a source of nutritional supplementation, the potential for these areas to facilitate disease transmission should be assessed.

Grassland Submodel. Although not all of the grassland/elk papers addressed direct impacts of elk on grasslands, they are part of a large body of information on a plant community that may be better understood than any other at YNP. Ungulate-grassland relations is perhaps the best understood of the conceptual model pathways due to a proliferation of studies initiated following a 1986 Congressional mandate to examine the issue of ungulate overgrazing within YNP. Most of the research conducted on YNP grasslands suggests that overgrazing does not occur in these communities. Nonetheless, we do not advocate a reduction in grassland research simply because it is well-researched, but instead, encourage the continuation of studies that build on the existing foundation of data and to better explicate the role of climate change, wolf restoration,

fire, and herbivory on northern range grasslands. Climate change could induce large-scale alterations in plant community structure and function in YNP that alters ungulate ecology. Climate-induced increases in fire frequency may alter landscape heterogeneity by creating patches of herbaceous forage in forested communities. Needless to say, climate should be monitored congruently with ungulate and forage abundance and distribution in order to assess its effect on ungulate-plant dynamics. Hobbs (1996) suggests that ungulate behavior must be integrated into predictive ecosystem models to understand patterns of forage selectivity across temporal and spatial scales. Climate-induced vegetation changes could have profound impacts on ungulate behavior as manifested in altered movement and habitat use patterns. The restoration of wolves in YNP has provided a unique opportunity for examining the impacts of a top predator on prey species, and in particular, elk. Determining the effects of wolf predation on elk habitat use would provide valuable insight for determining the influence top-down trophic effects have in regulating YNP's ecosystems. With the evolutionary tensions between elk and wolves restored, will elk spend more time evading wolves in forests and less time foraging in grasslands? What ecological implications would this reduction in grassland herbivory have on floral species composition, structure, nutrient cycling, and forage quality? Although elk may appear to benefit from the increased pulse of productivity exhibited by plants during spring and summer, improvements in elk condition have primarily been inferred through assessment of population growth. We suggest a GPS-based telemetry study that would allow researchers to correlate elk habitat use, forage quality, and elk condition as determined by direct observation and through assessment of physiological indices (e.g. blood, urine, and feces).

Human Submodel. Much of the controversy in YNP among scientists, resource managers, and the public in the last half-century has been focused on whether overabundant ungulates have caused ecological damage, and as to whether the current natural regulation policy can maintain the park's ecological integrity and meet public expectations. The reintroduction of the gray wolf in 1995 has restored the full complement of large carnivores to Yellowstone and may have rendered obsolete many of the arguments against natural regulation policy with regards to ungulate overabundance. In this respect, much of the research focused on ungulate-plant relations will need to be reexamined as carnivore-ungulate dynamics shift in conjunction with an expanding wolf population. Further, the effects of hunting elk on lands adjacent to YNP will need to be reexamined within the context of the new elk-wolf dynamic. Cassirer et al. (1992) indicated that elk disturbed by skiers suffered energetic costs associated with their flight from humans. Clearly, the impacts of recreational vehicles and activity, particularly snowmobiles, on elk distribution, foraging, and condition should be an important research consideration. Further, such recreational disturbances may have profound effects on predator distribution that in turn, relaxes top-down effects on ungulates and local plant communities. Thus, there is a need to study the effect of human activity on predator abundance and distribution and its effects on elk foraging and population ecology. We suggest that research be conducted that examines the effects of recreationists on wolf and grizzly spatial distribution to assess whether these disturbances alter the hunting success of these top carnivores, and ultimately the degree to which they regulate the Yellowstone elk herd. In contrast, elk habituation may result in several management problems ranging

from increased disease transmission to domestic animals and humans, to more frequent confrontational human-elk encounters (Thompson and Henderson 1998). Habituation may result from high-density elk populations and subsequent movement into human-dominated areas. Research is needed to develop strategies for describing and dealing with this potential problem.The ultimate success of most wildlife programs depends on the level of support within the community – especially that which involves large, conspicuous, and potentially dangerous animals. Such support depends on how well community interests are reconciled and the fairness of the public involvement process that produced the reconciliation (McClafferty and Parkhurst 2001). "Single-institution, top-down, command-and-control decision making will not suffice in true ecosystem management, for it can exclude the majority of persons and interests affected by the decision and can ignore relevant information and talents that could contribute to problem solving" (Carroll and Meffe 1997:364). We suggest a study that builds a foundation of ecological information and public involvement for issues related to the northern range elk herd. With this in mind, biologists and managers working within YNP must strive to assimilate themselves into a more diverse scientific community that includes economists, sociologists, land planners, and human demographers (Mace et al. 2001). Results from interdisciplinary research will help park officials better understand the mechanisms by which various human-related factors drive Yellowstone elk ecology and management.

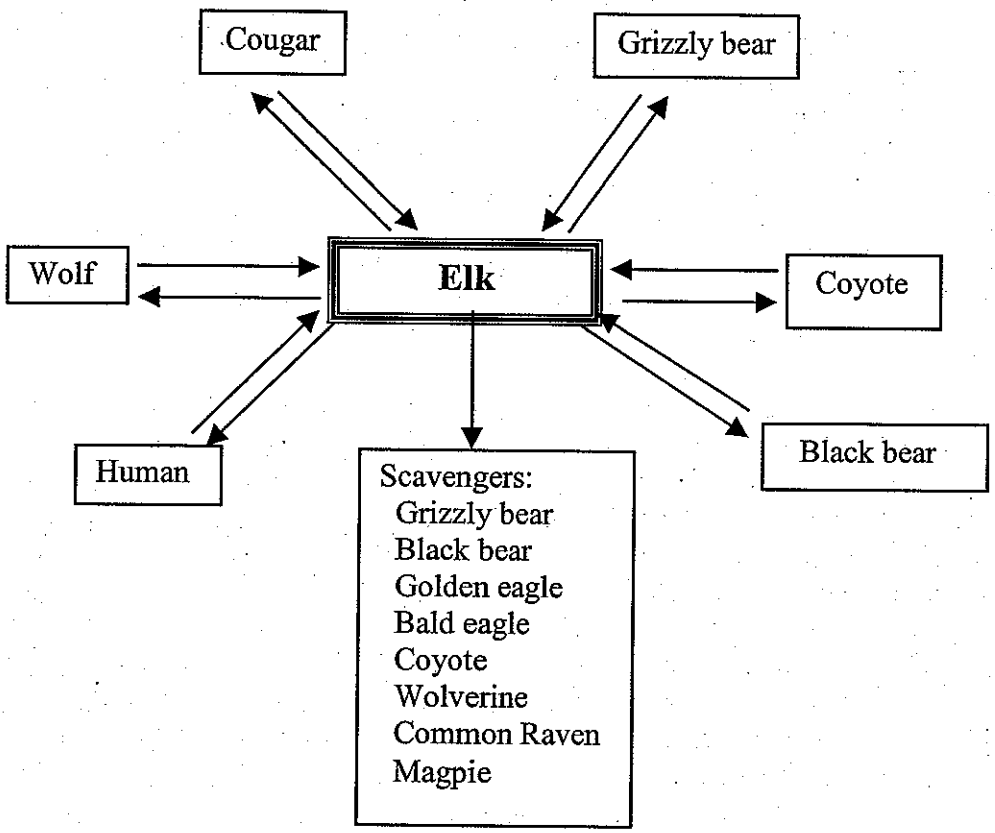
Parent Material Submodel. When viewed from a coarse resolution, Yellowstone National Park has two major parent material types that create distinct topography, soil conditions, and plant communities. First, the parent material for most of the park (Yellowstone Plateau) is rhyolite, a result of volcanism. The plateau was created through an outpouring of rhyolite that flattened the landscape that had resulted from previous sedimentation and erosion (Fenneman 1931). The parent material covering most of the northern range is sandstone (Shovic 1996). When viewed at a finer resolution, however, the distribution of parent materials across the northern range is much more heterogeneous than that of the rest of Yellowstone National Park (Shovic et al. 1996, Shovic 1996). Parent material has long been recognized as an important factor in regional soil development (Ramann 1928, Birkeland 1984). In turn, soil is a fundamental component of an ecosystem that influences the distribution, abundance, and productivity of biological communities (Bolen and Robinson 1995). Parent material, via its role in soil formation, can directly and indirectly influence the distribution of wildlife (Bolen and Robinson 1995). For example, parent material partly dictates the distribution and structure of vegetation in a landscape, and therefore, indirectly effects the distribution of and abundance of wildlife species associated with those communities (Leopold 1931). Research that addresses the "Parent Material → Soil Nutrients → Plant Communities (e.g. Willow) and "Parent Material → Soil Type → Plant Communities" pathways may provide data that allows for the development of vegetation profiles based on the presence of parent materials. Norland and Reardon (1996) suggested that parent material heterogeneity may influence distribution and abundance of northern range ungulates through its effects on sagebrush productivity, an important forage resource for wintering ungulates (Norland and Reardon 1996). They suggest that small-scale variation in soils to glacial material and landslide deposits create a patchwork of microsites with varying potential for sagebrush productivity. We suggest that predictive models be developed that attempt to determine

relationships among parent material, plant communities, and ungulate use, such as that which addresses relations between parent material/soil characteristics and aspen and willow communities at sites inside and outside of the park. Such work may provide further insight into the cause of the decline and limited growth of these plant communities inside park boundaries. Parent materials may exert direct influences on ungulate spatial distribution and habitat use in the form of mineral bearing licks (Knight and Mudge 1967, Geist et al 1983, Holl and Bleich 1987). Although geophagy by ungulates is well documented (Jones and Hanson 1985), patterns of mineral lick use and their nutritional importance to ungulates have yet to be addressed in Yellowstone. However, their potential as a source of minerals for ungulates has been suggested (Tracy and McNaughton 1995). Despite the seemingly important role parent material has in influencing plant communities, researchers have largely failed to incorporate this environmental factor into their studies. Shovic (1996) wrote, "Given the character of these environmental variables [landform, soils, and vegetation] the intensity of their effect may confound a cursory analysis of the apparent effects of present wildlife use." Such obfuscation has likely impacted past studies in YNP that have examined consumptive and trampling-induced effects of ungulates on vegetation, soil processes, and erosion. In order to gain a more complete understanding of ungulate ecology on the northern range, we believe it is imperative that future study designs take into account the driving influences parent materials have on the GYE.

Predator Submodel. Increased numbers of elk carcasses provided by a growing wolf population will likely provide more food for scavengers (raven, magpie, eagles, bears, coyote) than that available prior to wolf reintroduction. New and ongoing studies should examine changes in populations and distributions of scavengers associated with this predation phenomenon (Fig. 16). Additionally, the effects of inter-specific competition between wolves and other elk predators should be examined (Fig. 16). While immediate behavioral responses of ungulates to wolves have been documented (Berger et al. 2001), additional study is needed to examine spatial and temporal changes in elk herds in response to wolf predation. Research should also focus on determining the degree to which the YNP elk population structure fluctuates in response to differential predation by wolves of adult elk versus calves during severe winters (Carbyn 1983, Huggard 1993, Mech et al. 2001). Many papers acknowledge the over-riding influence of human interests in re-establishing natural predator-prey relations in YNP, yet we did not find literature that examined the aspect of human dimensions in managing ungulates and predators in the GYE. This should become an on-going research project due to the importance of public involvement in developing park policy and in determining the trajectory of surrounding land uses. For example, research could examine whether removal of wolves by humans (e.g., hunting seasons out-side YNP, depredation removals,_or poaching) alters the sex-age structure of Greater Yellowstone wolf populations? If so, will this result in a change in the way wolves affect the population dynamics of YNP elk, as suggested by Murphy (1998) with regards to mountain lion-prey relations? With only one known black bear population study having been conducted in YNP (Barnes and Bray 1967), it is easy to see why Knight et al. (1999) referred to this species in YNP as "the forgotten black bears of Yellowstone". Prior to wolf reintroduction, approximately one-third of elk calves died due to predation by grizzly

bears, black bears, and coyotes (Singer et al. 1997). Predation by these species was not thought to limit elk population growth in YNP. What role do bears play in regulating elk in Yellowstone now that wolves have been reintroduced to the system? Will resource partitioning occur between bears and wolf? If so, will predation be spatially, temporally, or demographically segregated to reduce interspecific encounters between bears, wolves, and other predators? In the presence of wolves will predation on elk by bears become additive mortality and thus contribute to limiting the YNP elk population?

Figure 16. Illustration of the central role elk play in the Yellowstone predator and scavenger guilds.

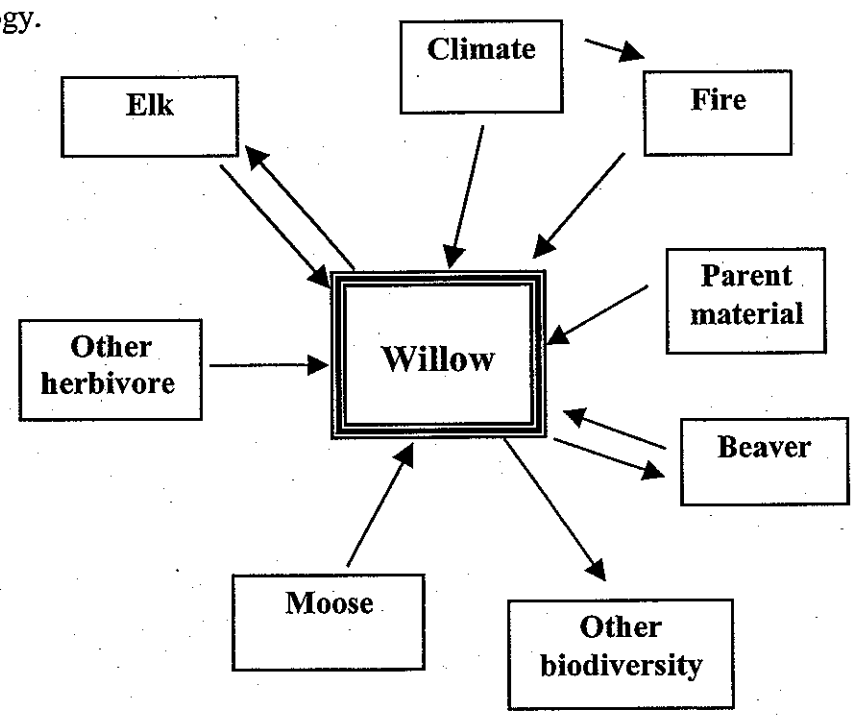


Topography Submodel. As indicated by our conceptual model, topography has the potential to be an important driver of elk ecology in YNP. However, topography's importance in shaping elk ecology is often confounded by its interplay with climate, parent material, and local plant communities. While many studies have taken into account potential topographic effects on elk ecology, further investigation is needed to address a number of pathways and feedback loops. Only 6 of 43 pathways and 2 of 6 feedback loops were at least partially addressed in the reviewed literature. Investigation into the effects of topography and its interplay with climate and hydrology on a number of plant communities important to elk, such as aspen and willow, are needed. The challenge to researchers will be to elucidate the relative importance that topographic components (e.g., aspect, slope, and elevation) have in temporally and spatially influencing elk behavior

with regards to the avoidance of predators and human disturbance, forage procurement, herd social dynamics, and alleviating weather extremes.

Willow Submodel. Known defoliators of willows, such as beetles and snowshoe hares, have not been examined in the context of their potential impacts on willow. Similarly, even the most controlled experiments did very well to measure differences in willow structure and abundance, but, at best, the researcher inferred herbivory by elk (via elk relative abundance) even though such utilization was seldom observed directly. Although elk consume willow, there are several other species that do as well. Even though moose and white-tailed deer are relatively uncommon in YNP, they tend to preferentially browse willow. Thus, even low numbers of these two species may have negative effects on willow height, canopy coverage, and reproduction. Research is needed to elucidate the contribution and relative importance of a variety of consumers to evaluate their regulation of the abundance and distribution of willow. The effects of interacting or co-occurring factors on the status of Yellowstone willows have been well established. Identifying the relative importance of any one factor, however, has been problematic. Our overall conceptual model suggests a variety of biotic and abiotic forces that might influence willow growth and reproduction (Fig. 2). However, the equivocal nature of the literature, or the linkages among factors that may influence willows are so intertwined as to prevent, to date, the weighting of these individual factors in a conceptual model. At best, we are confident that herbivory and abiotic factors combine to influence willow and offer a more simplistic conceptual model that reflects the ability of existing literature to describe a complex system (Fig. 19).

Figure 19. A simplistic conceptual model that reflects the ability of existing literature to describe the influence of various biotic and abiotic factors on northern range willow ecology.



We suggest that future studies address the importance of ungulate herbivory in an experimental fashion that isolates the activities of single species and that also allows the measurement of relative influence of abiotic processes such as alluviation, hydrology, and other climatic factors on willow in YNP. In particular, such research is needed to examine the many suggested hypotheses regarding willow, elk, and beaver interrelations. For example, it has been suggested that over-browsing by elk caused the decline of beaver in YNP (Kay 1997), and that this decline has rendered the species ecologically extinct within the park (Kay 1997, Singer et al. 1998). Singer et al. (1998) suggested that beaver decline in Yellowstone, and subsequent changes in hydrological patterns, may have exceeded a threshold value for willow persistence and recruitment by reducing rates of photosynthesis and growth (Singer et al 1998). Further, reduced chemical defenses in height-suppressed willows, combined with a reduced biomass potential, both due to climate and water table reductions, may act to keep willows in a heavily browsed and height-suppressed condition across a wide range of elk densities (Singer 1996a). Clearly, rigorously designed studies are needed to assess the interplay among the aforementioned factors to better understand willow ecology in YNP.

RESEARCH PRIORITIZATION

We identified research gaps within each submodel and quantified the relative inferential strength and scope of topics (Table 4 and Figure 20). Our findings revealed that with regard to elk in YNP, relations with beaver have yet to be scientifically addressed, while geothermal features/events, parent material, and topographic influences have been inadequately researched in comparison to other model components. In contrast, elk relations with grassland, aspen, coniferous forest, and fire have been relatively well studied in the GYE; the former topic having drawn considerable political attention in the 1990's, and the later 3 the result of opportunistic research that followed the 1988 fires.

Research priorities, however, are not determined solely by the need for scientific knowledge. Management issues that involve public and political concerns and needs are an important consideration that must often be incorporated into resource allocation and research prioritization schemes. To demonstrate the potential utility of integrating our understanding of existing research gaps within the conceptual model with management issues, we developed an "urgency" index that addressed issues of temporal dynamics and issues of management concern in the GYE within the past two decades. We subsequently used a two-axes system based on the research gap and urgency values to ordinate submodels and categorize them for research prioritization (Figure 21). As such, we developed a management index based on the relative temporal dynamics of our submodels and those issues of recent concern to the GYE (Table 5). Our elk-centric model indicated those topics concerning beaver, disease, humans, predation, and competition should receive the highest research priority (Table 6) and those involving elk relations with grasslands, topography, parent material, and geothermal features/events should receive the least. In conclusion, we recommend the following fifty elk-centric research priorities, in priority order by fourteen elk-centric submodels, at Yellowstone National Park based on research gaps, information needs and management urgency identified through the application of this Comprehensive Rapid-assessment for Research Agenda Development.

1. Beaver

- Interactive effects of elk and beaver on riparian community vegetation structure and function.

2. Disease

- Development of safe and effective vaccine for brucellosis in GYA elk.
- Epidemiology of brucellosis in free-ranging GYA elk.
- Epidemiology of chronic wasting disease in free-ranging GYA elk.
- Long-term prevalence of brucellosis in GYA elk.
- Long-term prevalence of chronic wasting disease in GYA elk.
- Role of GYA elk meta-population dynamics in contagion and spread of chronic and emerging diseases.
- Role of GYA elk parasites in disease and predation vulnerability.

3. Human

- The role of human harvest of elk outside the park on elk population dynamics.
- The role of human harvest of predators outside the park on elk population dynamics.
- The seasonal effects of park visitor use patterns on elk distribution, foraging and condition.
- The role of human habitats (e.g. park developed areas and travel corridors) on elk habituation, distribution, foraging and condition.

4. Predators

- Response of scavenger guild population dynamics to elk carrion availability.
- Effects of inter-specific dynamics (e.g. competition, exclusion, facultative) among a multi-carnivore guild on elk population dynamics.
- Response of elk behavior (e.g. vigilance, non-foraging time budgets, multi-scale habitat selection) to predator presence and absence.
- Responses (spatial and temporal) of elk population structure to interactive effects of winter severity, hunting outside the park, and predation.
- Effects of predator removals outside the park on elk population dynamics.
- Cause specific mortality rates of elk calves in the presence of a multi-predator guild.
- Is predation on elk by a multi-predator guild segregated spatially, temporally and demographically to reduce inter-specific predator interactions?

5. Competition

- Does scale-dependent inter-specific niche separation and competitive exclusion occurr at population levels below ecological carrying capacity?

- Role of elevationally and seasonally progressive vegetation phenology in mitigating or facilitating intra- and inter-specific competition within a multi-large herbivore guild.
- Effects of winter severity and winter range expansion on intra- and inter-specific competition within a multi-large herbivore guild.

6. Climate

- Expand long-term climate monitoring on seasonally important elk habitats.
- The effects of summer precipitation on summer elk calf recruitment.
- The effects of seasonally variable snow parameters (e.g. depth, snow water, crusting, etc.) on elk foraging ecology and predator-prey dynamics.

7. Willow

- Experiments to generate mechanistic explanations of the interactive effects of herbivory by a multi-large herbivore guild on willow abundance, distribution and recruitment.
- Experiments to generate mechanistic explanations of interactive effects of elk herbivory, beaver, and abiotic factors in limiting willow abundance, distribution and recruitment.
- Experiments to generate mechanistic explanations of the effects of willow secondary compounds on palatability for elk and as chemical defenses against herbivory by elk.

8. Fire

- Scale-dependent effects of post-fire tree-fall patterns on elk habitat availability and selection.
- Scale-dependent effects of post-fire succession patterns on elk habitat availability and selection.
- Short-term fire effects on nutritive value of important elk forages.
- Effects of fire heterogeneity on elk energetic costs-benefits.
- Effects of elk herbivory on fine-scale fire susceptibility and return intervals.

9. Aspen

- Relative importance of aspen to elk nutrition and condition.
- Scale-dependent interactive effects on foraging by elk and other large and small herbivores on aspen distribution and abundance.
- The effects of elk-predator dynamics on aspen community structure (e.g. abundance, distribution, recruitment) and function (e.g. release from herbivory, nutrient and water cycling).

10. Coniferous Forest

- The scale-dependent role of forest landscape heterogeneity and indices (fractal, edge, patchiness, etc.) on elk habitat selection and predator-prey dynamics.
- The role of coniferous forest cover in mitigating elk physiological vulnerability to climatic extremes.

11. Geothermal

- The scale-dependent role of surficial geothermal activity on density-dependent and density-independent elk habitat selection and population dynamics.
- The interactive and scale-dependent role of surficial geothermal activity, winter severity, and predation vulnerability in density-dependent and density-independent elk population dynamics.
- The facultative role of surficial geothermal activity in contagion and spread of chronic and emerging elk diseases.
- The effects of surficial geothermal activity on elk foraging ecology.
- The potential for multi-trophic level effects arising through elk consumption of toxic elements at surficial geothermal sites.

12. Parent Material

- The role of parent material in limiting the distribution and abundance of important elk winter range woody vegetation, shrubs and residual graminoid forage.
- The direct and indirect effects of mineral licks on seasonal elk distribution and habitat selection, migration pathways, and elk calving ground selection.

13. Topography

- The interactive effects of topographic, climate and hydrologic variability on elk habitat suitability and selection.
- Scale-dependent effects of topographic variability (e.g. aspect, slope, elevation) on temporal and spatial patterns of elk foraging ecology, habitat selection, and predator-prey dynamics.

14. Grassland

- Continue long-term research that builds upon the existing foundation to explicate long-term feedback effects of climate change and fire on grassland structure and function to elk habitat limitations.
- Continue long-term research that builds upon the existing foundation to explicate long-term effects of elk herbivory on grassland community structure and function, energy flow, and nutrient cycling.
- Fine-scale habitat selection by elk in grassland communities in response to topographic, forage availability, and forage nutritive value variability.

Table 4. Research gap values (RGV) for the 14 submodels of the elk-centric conceptual model . Numbers in parentheses refer to the relative rank of each submodel within the category with higher numbers indicative of higher rank. (IP) inferential power; (Prop Path) proportion of pathways addressed in each submodel.

Submodel	# Papers	Mean IP	Prop Path	RGV
Beaver	0 (14)	-- (14)	0.0 (14)	52
Geothermal	3 (11.5)	2.0 (5.5)	.13 (12)	29
Parent Material	1 (13)	1.0 (1)	.07 (13)	27
Topography	9 (8.5)	2.1 (7)	.18 (11)	26.5
Disease	8 (10)	2.6 (11)	.50 (5.5)	26.5
Human	10 (6.5)	2.4 (9)	.25 (10)	25.5
Competition	3 (11.5)	2.6 (11)	.66 (2)	24.5
Willow	9 (8.5)	2.0 (5.5)	.33 (8.5)	22.5
Climate	17 (4)	2.6 (11)	.60 (4)	19
Predator	19 (3)	2.7 (13)	.63 (3)	19
Forest	10 (6.5)	1.8 (2.5)	.33 (8.5)	17.5
Fire	32 (2)	2.3 (8)	.43 (7)	17
Aspen	11 (5)	1.9 (4)	.50 (5.5)	14.5
Grassland	39 (1)	1.8 (2.5)	.80 (1)	4.5

Table 5. Urgency index (URG Score) for the 14 submodels of the elk-centric conceptual model. Temp Scale is the relative temporal dynamics of the submodel (LT, long-term; century); MT (medium-term; decade); ST (short-term; annual). Temp Score refers to the relative ranking of the Temp Scale where 3 is given highest urgency. Management refers to the subjective ranking of management topics within the past decade, with 5 given the highest urgency. URGV is the sum of the Temp Score and Management categories.

Submodel	Temporal Scale	Temporal Score	Management Priority	URGV
Predator	ST	3	5	8
Human	ST	3	4	7
Disease	ST	3	4	7
Grassland	ST	3	3	6
Competition	ST	3	3	6
Fire	MT	2	4	6
Climate	LT	1	5	6
Willow	MT	2	3	5
Aspen	MT	2	3	5
Beaver	MT	2	2	4
Coniferous Forest	MT	2	2	4
Parent Material	LT	1	1	2
Geothermal	LT	1	1	2
Topography	LT	1	1	2

Table 6. Priority score of submodels as determined by relative rank of research coverage and management urgency.

Submodel	RGV	URGV	Priority Score
Beaver	52	4	208.0
Disease	26.5	7	185.5
Human	25.5	7	178.5
Predator	19	8	152.0
Competition	24.5	6	147.0
Climate	19	6	114
Willow	22.5	5	112.5
Fire	17	6	102.0
Aspen	14.5	5	72.5
Forest	17.5	4	70.0
Geothermal	29	2	58.0
Parent Material	27	2	54.0
Topography	26.5	2	53.0
Grassland	4.5	6	27

Figure 20. Relative rank of research gaps within the elk-centric model.

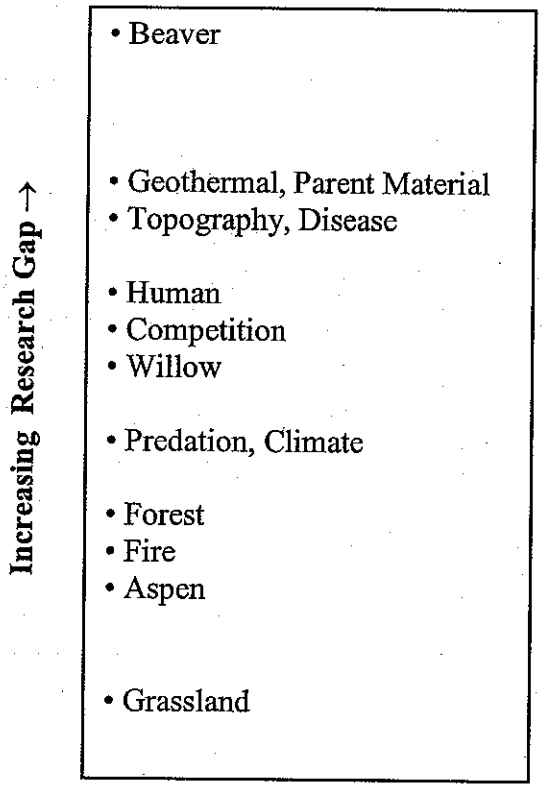
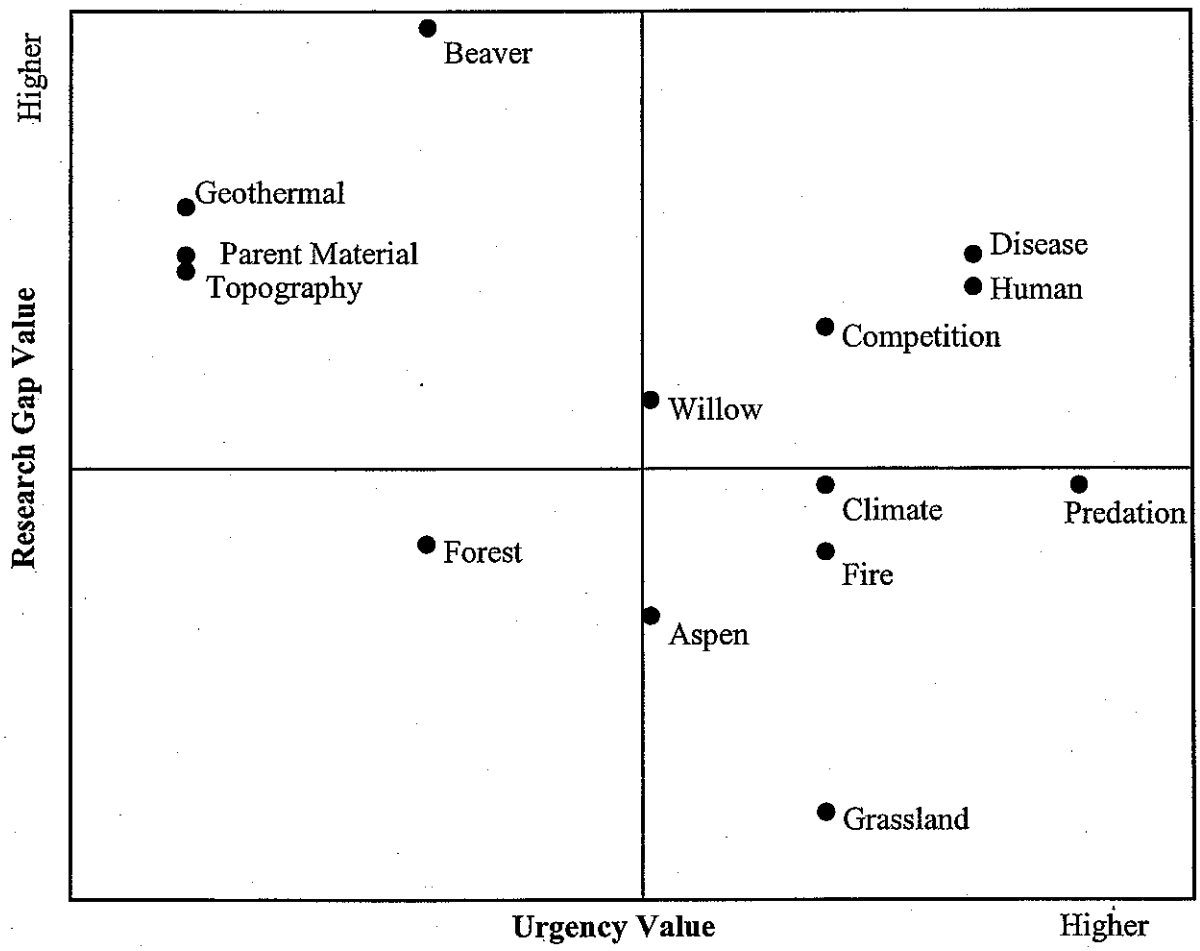


Figure 21. Relative research priorities among submodels of the elk-centric conceptual model as determined by urgency and research gaps values.



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Wright, R.G. 1998. A review of the relationship between visitors and ungulates in national parks. Wildlife Society Bulletin 26:471-476.

Wu, Y., M.G. Turner, L.L. Wallace, and W.H. Romme. 1996. Elk survival following the 1988 Yellowstone fires: A simulation experiment. Natural Areas Journal 16:198-207.

Yochim, M.J. 2001. Aboriginal overkill overstated: Errors in Charles Kay's hypotheses. Human Nature 12:141-167

ANNOTATED BIBLIOGRAPHY

Augustine, D.J. and D.A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology 82: 3149-3162.

Topic(s): Grassland
Category: Experimental Study (1) – Journal Article
Purpose: To determine how Yellowstone's migratory ungulate populations may structure the spatial pattern of soil N properties.
Conclusions: The focus of this study was spatial variation in plant and soil properties. Across the three study sites, grazers did not alter the total amount of variation. Native, migratory ungulates inhabiting Yellowstone's northern winter range exert a strong effect on ecosystem dynamics by accelerating rates of primary productivity and nitrogen cycling. The results demonstrate that in addition to the effects of topography and vegetation on spatial patterning of resource availability, biotic components of ecosystems such as large herbivores not only respond to resource heterogeneity, but also play a significant role in generating observed patterns. Findings show herbivory also modifies soil heterogeneity at small spatial scales, increasing the amount of variability in the soil environment experienced by a plant individual. Root dynamics may be a particularly important determinant of soil N distribution in Yellowstone grasslands because root biomass was much greater and more evenly distributed than above ground plant biomass.
Hypotheses: The following hypotheses were tested:
Ungulates increase fine-grained variability (e.g., variation across distances less than 10 cm in soil N properties. (SUPPORTED)

1) Grazing alters the distribution of homogenous patches with respect to N mineralization potential (SUPPORTED)
2) The spatial distribution of N in plant biomass displayed no consistent difference between grazed vs ungrazed plots (SUPPORTED)
3) Ungulates influence species diversity of grasslands only at small spatial scales (SUPPORTED)

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Topic(s): Grassland
Category: Literature review (5) - Journal article
Purpose: To review studies of ungulate effects on plant community composition and ecosystem processes.
Conclusion: High levels of nutrient inputs or recycling and an intermittent temporal pattern of herbivory (often due to migration) are key factors increasing the

regrowth capacity of palatable species and hence maintaining their dominance in plant communities supporting abundant herbivores. Differences among ecosystems in the role played by ungulate herbivory result from the relative strength of these factors enhancing plant tolerance to herbivory and limiting foraging selectivity. Anthropogenic changes in these factors (e.g., alteration of migration patterns) may alter the effects of ungulates on plant communities and ecosystem processes.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) The combination of seasonal migrations, ungulates foraging in large, dense herds, high input rates of nitrogen to the soil system on growing-season ranges, and regular plant disturbance by trampling limit the abundance of unpalatable species in plant communities.
2) Elk selectivity of palatable, herbivore-tolerant plant species will reduce predation upon less herbivore-tolerant plant species and, thus, decrease the likelihood of invasion by unpalatable plant species.

Balling, R. C., G. A. Meyer, and S. G. Wells. 1992. Climate change in Yellowstone National Park: is the drought-related risk of wildfires increasing? Climatic Change 22:35-45.

Topic(s): Climate, Fire, Forest [anecdotal (6)]

Category: Observational study (2) - Journal article

Purpose: To (a) determine the relationship between Yellowstone wildfires and local climate variations during the period of historical records, (b) examine trends in fire-related climate variables, and (c) compare observed trends in fire-related climate variables in the Yellowstone area to the predictions made by a number of climate models for the 2 x CO2 condition.

Conclusion: The climate change toward increasing aridity, and therefore, a climate-induced increase in the fire hazard, is a very real feature in the historical records for the Yellowstone National Park area. Fire regimes in these forests are characterized by stand-replacing fires which occur at intervals of 150-300 years or more, and flammability tends to increase as stands approach maturity over these intervals. Climate changes in Yellowstone National Park are characterized by (a) increasing temperatures in the fires season, (b) decreasing precipitation in the antecedent season and, (c) a trend to drought conditions in the antecedent season. While the risk of wildfire in the park is only partially related to climate, the trend of the past century is significant and should be carefully monitored in the immediate future

Hypotheses: No hypotheses were tested or suggested.

Berger, J., and S.L. Cain. 1999. Reproductive synchrony in brucellosis-exposed bison in the southern greater Yellowstone ecosystem and in noninfected populations. Conservation Biology 13:357-366.

Topic(s): Disease
Category: Experimental study (1) - Journal article
Purpose: To assess the potential effects of brucellosis on reproductive synchrony in bison.
Conclusion: Bison herds with or without brucellosis exhibit no differences in timing of reproductive synchrony. An interaction between food quality, and infection in elk, complicate the spatial-temporal relations among bison, elk, and cattle.
Hypotheses: The following hypothesis was tested:
1) Reproductive synchrony differs between *Brucella*-exposed and non-*Brucella*-exposed bison populations.

The following hypothesis /prediction was suggested:
1) Food provisioning of bison and elk during winter may reduce aborted fetuses or brucellosis transmission to domestic stock when compared with populations in poorer physiological conditions.

Bergstrom, R. C., and R. Robbins. 1979. Lungworms (*Dictyocaulus viviparus*) in various age classes of elk (*Cervus canadensis*) in the Tetons. Pages 222-223 in M. Boyce and L. Hayden-Wing, editors. North American elk, ecology, behavior, and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Disease
Category: Observational study w/o mechanistic explanation (3) - Book chapter
Purpose: To examine lungworm infection in various age classes of elk in the Tetons (GYE).
Conclusion: Calves were not infected with lungworm until 6 months of age. Yearling elk had the highest prevalence (76%) of all age classes and usually carried the greatest number of worms. Infection rates varied seasonally within all age classes. Two of three distinct elk herds in western Yellowstone Park, had winter infection rates of 9-16%. One group was uninfected.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Lungworm parasites affect migration patterns of elk.
2) Lungworm infection rates in elk vary seasonally and among age classes.

Boyce, M. 1991. Natural regulation or the control of nature? Pages 183-208 in R. R. Keiter and M. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Human
Category: Literature review (5) - Book chapter
Purpose: To evaluate alternative priorities for wildlife management in the GYE. To review relevant ecological principles in order to clarify some of the confusing literature that addresses wildlife ecology in Yellowstone.
Conclusion: The greatest controversy regarding the application of ecological-process management in the GYE surrounds the management of ungulates, particularly elk, on Yellowstone's northern range. The author discusses why he feels four signs of natural regulation failure in YNP are inappropriate and misleading. Increasing the scientific rigor of understanding of the GYE will enhance its management.
Hypotheses: No hypotheses were tested or suggested.

Boyce, M. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234-269 in R.S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. Scientific Monograph NPS/NRYELL/NRSM-93/22.

Topic(s): Predator
Category: Predictive model (4) - Gray literature
Purpose: To predict the probable consequences of gray wolf reintroduction on ungulate populations in Yellowstone National Park. This model allows the user to choose several possible management scenarios, and by manipulating alternatives, explore the consequences of different management actions. The purpose of the model is not to offer recommendations about whether wolf recovery should take place, but rather to provide resource managers with an additional tool that will assist them in making such a decision.
Conclusion: Computer simulations indicate that wolf recovery will result in a reduction in both the mean and variance in ungulate numbers.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Hunting mortality is additive to density dependent mortality of elk in YNP (i.e. elk movements out of the park are more likely when population size is high, thereby exposing elk to more hunters in those years).

Boyce, M. 1995. Anticipating consequences of wolves in Yellowstone: model validation. Pages 199-210 *in* Carbyn, L.N., S.H. Fritts, and D.R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35.

Topic(s): Predator
Category: Predictive model (4) – book chapter
Purpose: To describe an expanded simulation model of wolf-prey dynamics for YNP and to discuss approaches for validation of the model.
Conclusion: The northern range elk population is expected to decline 5-20% during the next 100 years following wolf recovery. Wolf recovery will be more dependent on management than biological considerations. Model predictions suggest that wolves will reduce the average annual population size and annual harvest of elk. Wolf predation may eliminate the need for controversial elk harvest in Grand Teton National Park.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) The abundance of elk in YNP may reduce prey switching by wolves.
2) Prey switching by wolves may occur in the Madison-Firehole region of YNP where the biomass of bison is greater than the biomass of elk.

Boyce, M. S. 1996. The Aldo Leopold Memorial Lecture: if I were superintendent. Pages 201-208 in Jason Greenlee, editor. Ecological implications of fire in greater Yellowstone. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Human
Category: Literature review (5) - Gray literature
Purpose: To speculate on how to use the research results reported at the 1996 International Association of Wildland Fire conference to better manage the GYE.
Conclusion: Ecological-process management should be the direction of the GYE. One of the most effective ways to improve natural resource management programs is through an iteration of science and management.
Hypotheses: No hypotheses were tested or suggested.

Boyce, M.S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin 26:391-398.

Topic(s): Human
Category: Literature review (5) - Journal article
Purpose: To re-examine the arguments for controlling ungulate populations in national parks.
Conclusion: Fluctuation in ungulate populations with consequent influences on vegetation is one of the ecological processes that shape ecosystems.

Ecological-process management has provided an understanding of how the ecological systems function in natural areas and will assist with wildlife management inside and outside national parks.

Hypotheses: No hypotheses were tested or suggested.

Boyce, M. S., and E. H. Merrill. 1996. Predicting effects of 1988 fires on ungulates in Yellowstone National Park. Pages 361-366 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. National Park Service Technical Report NPS/NRYELL/NRTR/96-01.

Topic(s): Fire

Category: Predictive model (4) - Gray literature

Purpose: To extrapolate data from the authors' previous work on ungulate population dynamics in Yellowstone to construct computer projections of the consequences of 1988 fires on size of future elk and bison populations.

Conclusion: An increase in both elk and bison wintering populations will occur within the park following the 1988 fires in summer range.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Elk and bison wintering populations within the park will increase in response to the projected increase in summer range quality following the 1988 fires.

Cassirer, E.F., D.J. Freddy, and E.D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375-381.

Topic(s): Human, Topography, Forest

Category: Observational study (2) - Journal article

Purpose: The objectives of this study were to measure the immediate movements of elk when disturbed by cross-country skiers, to assess energy costs associated with these movements, and to identify factors that may influence elk behavior.

Conclusion: Energy expended moving away from skiers represented approximately 5.5% of an estimated daily energy expenditure for elk in winter. Overall, both flight distance and movement increased in elk disturbed outside the developed area. This may be due to elk habituating to predictable human activity. The authors recommend that when skier activity is located on elk winter range that it be concentrated into as small an area as possible.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Elk temporarily move up in elevation to steeper slopes and closer to forested areas when disturbed by skiers.

Chadde, S. W., and C. E. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. Pages 231-262 *in* R. R. Keiter and M. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Willow, Human, Beaver [anecdotal (6)], Competition [anecdotal (6)], Aspen [anecdotal (6)], Topography

Category: Observational study (2) - Book chapter

Purpose: To examine historical changes in willow communities on the northern range and evaluate the factor or factors responsible for the changes in riparian habitats.

Conclusion: The authors contend that a comparison of willow stands both inside and outside fenced exclosures demonstrates that herbivory, primarily by elk, has repressed willow production. They use this as evidence for rejecting the "natural-regulation" hypothesis based on Houston's (1976) proposed set of criteria. In their opinion, the decline in willow and beaver demonstrates retrogressive plant succession and competitive exclusion of sympatric herbivores. They suggest the system is in a state of nonequilibrium and cannot be regulated naturally. The authors conclude that their findings reject the criteria proposed by Houston for evaluating the "natural-regulation" hypothesis.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Tall-willow communities that are now nearly absent, were once common on the northern range.
2) Willow stands are affected by ungulate browsing.
3) Willow stands at higher elevations are less affected by ungulate browsing than lower elevation stands because of greater snow depth.
4) Repeated ungulate browsing on willow results in both willow height and canopy-coverage reduction.
5) Beaver have virtually been eliminated from the northern range due to interspecific competition with elk.
6) Browsing by elk and moose prevent willow from expressing their full biological height and canopy-coverage on the northern range.
7) Beaver need tall willows or aspen as food and dam-building materials
8) By preventing aspen and willows from growing into sizable plants, elk and moose eliminate beaver foods and beaver.

Christensen, N.L., J.K. Agee, P.F. Brussard, J. Hughes, D.H. Knight, G.W. Minshall, J.M. Peek, S.J. Pyne, F.J. Swanson, J.W. Thomas, S. Wells, S.E. Williams, and H.A. Wright. 1988. Ecological consequences of the 1988 fires in the greater Yellowstone area. Final report, The Greater Yellowstone Postfire Ecological Assessment Workshop.

Topic(s): Fire, Aspen [anecdotal (6)], Forest [anecdotal (6)]
Category: Literature review (5) – Gray literature
Purpose: To (1) provide a general account of the 1988 fires that addresses their ecological impacts and significance with respect to past, current, and potential future management practices, (2) provide scientific documentation of the likely ecological consequences of the 1988 fires, and (3) serve as a guide to outline research needs and opportunities.
Conclusion: The authors concluded that a program of research on the 1988 fires should be initiated. This program should include an ecosystem approach integrating many research projects, a landscape approach utilizing geographic information systems, and monitoring key system features and processes. The scale and heterogeneity of the Yellowstone fires provide a unique opportunity for developing insight into future wilderness management.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) The loss of surface organic matter, particularly in coniferous forests may dramatically alter soil physical characteristics.
2) The loss of humus may result in some reduction of water infiltration and could alter nutrient exchange capacity on sites where soil heating was intense.
3) Fire-caused changes in soil surface microclimate can adversely affect plant growth.
4) Tree establishment and growth may be poor or absent on sites where soil temperatures were high or the duration of heating was long.
5) Intense heating is generally confined to small sites (e.g., burnt logs) and microbial recolonization will likely be rapid from adjacent moderately burned areas.
6) The soil and microclimatic conditions following fire favor the establishment and growth of a variety of native herb and shrub species.
7) Big sagebrush abundance may decrease because it does not sprout following a fire.
8) Sprouting grasses and forbs increase until new sagebrush seedlings become established and grow to maturity, perhaps 15-30 years later.
9) Forest regeneration will be slower where aspen was not present in the coniferous forests.
10) Improved forage conditions resulting from the fires on summer range will enhance winter survival.

Cole, G.F. 1969. Elk and the Yellowstone ecosystem. Unpublished Research Note, National Park Service, Yellowstone National Park, Wyoming, USA. 14pp.

Topic(s): Human, Predator
Category: Anecdotal (6) - Gray literature
Purpose: To describe how elk may be naturally regulated within YNP and how this coincides with the conservation goals of the park.

Conclusion: The decline in native predators and restriction of free-ranging movements by elk presented a human-caused problem to natural regulation within YNP. Yearly quota hunts outside the park may be used so elk within park boundaries could be naturally regulated.

Hypotheses: No hypotheses were tested or suggested.

Cole, G.F. 1971. An ecological rationale for the natural and artificial regulation of native ungulates in parks. Transactions of the North American Wildlife and Natural Resources Conference 36:417-425.

Topic(s): Human

Category: Literature review (5) - Journal article

Purpose: To show that the objectives of preserving or restoring the aesthetic and scientific values of representative natural ecosystems or their community units require broad ecological considerations. The rationale for artificially regulating wild ungulates in parks was not always consistent with the objectives or present management policies of natural areas.

Conclusion: The rationale for relying on natural processes to regulate native ungulate populations in parks is that the animals are not causing unnatural trends in biological succession, or the antithesis of the rationale for artificial regulation. A fundamental consideration in applying this rationale is that the presence of humans must be distinguished from their significant ecological effects.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Populations of native ungulates cannot, without overriding successional influences or habitat limitations imposed by man, progressively reduce food sources that limit their own densities.
2) In the absence of human restrictions on their free-ranging use of ecologically complete habitats, native ungulates do not cause retrogressive or secondary succession.

Cole, G.F. 1972. Grizzly bear-elk relationships in Yellowstone National Park. Journal of Wildlife Management 3:556-561.

Topic(s): Winter Severity, Predator

Category: Predictive model (4) - Journal article

Purpose: To demonstrate how grizzly bear predation and competitive scavenging are natural processes that contribute to the regulation of Yellowstone's elk population.

Conclusion: Grizzlies are sometimes highly cursorial predators. Subadult or subordinate young bears appeared to be the most effective predators on elk. The justifications for maintaining a representative grizzly population within YNP are to (1) maintain natural equilibriums among interacting secondary consumers, (2) maintain natural relationships between

interacting secondary and primary consumers, and (3) retain the unique scientific values of ecological systems with an intact native biota.

Hypotheses: No hypotheses were tested or suggested.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71-82.

Topic(s): Grassland

Category: Observational study (2) - Journal article

Purpose: In this comparative study, the author uses estimates of shoot and root standing crops and nitrogen concentrations within exclosures to assess more precisely the effects of elk grazing on herbaceous plant communities.

Conclusion: The most pronounced effects of grazing were reductions of dead grass and litter occurs during the winter. Nitrogen concentrations of live and dead grass were increased from winter grazing. The net effects of winter grazing appeared to be a redirection of biomass flow from decomposers into elk, accompanied by an enhanced rate of N recycling back to elk. The fact that perennial root biomass persisted, indicated the net consequences of winter grazing for these plants.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Grazing reduction of standing dead material and litter affect microclimate and nutrient cycling.
2) Standing dead grass is important when June is very dry because it prevents accelerated soil evaporation and increased temperatures above those optimal for photosynthesis.
3) Greater root investment enhances resistance of plants to spring grazing.
4) Grazing increases shoot nitrogen concentrations in grasses.
5) Grazers increase nutrient turnover rates by returning mineral nitrogen to the soil in a more readily decomposable form, thereby bypassing slower litter decomposition.

Coughenour, M. B. 1994. Elk carrying capacity on Yellowstone's northern elk winter range: preliminary modeling to integrate climate, landscape, and nutritional requirements. Pages 97-111 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Grassland, Climate

Category: Predictive model (4) - Gray literature

Purpose: To (1) develop a dynamic model for elk carrying capacity (K) that is nutritionally based and constrained by snow and (2) determine the level and spatial distribution of herbivory that elk impose on winter range forage. These are first steps to assess limitations on elk population size

that may arise from spatial and temporal variations in the quantity and quality of available forage.

Conclusion: The effects of spatial and temporal variations in forage quality and quantity, effects of snow depth on available foraging area, and elk nutritional requirements must be synthesized to calculate spatial and temporal patterns of herbivory.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Elk avoid areas with greater than 40 cm of snow.

Coughenour, M. B., and F. J. Singer. 1991. The concept of overgrazing and its application to Yellowstone's northern winter range. Pages 209-230 *in* R. R. Keiter and M. Boyce editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Grassland, Human

Category: Literature review (5) - Book chapter

Purpose: To examine the concept of overgrazing as applied to Yellowstone and to reveal how the concept evolved in relation to changes in natural conditions, changes in human influence on the system over time, and scientific advances. The authors compare concepts of overgrazing as used by a range manager, a wildlife manager, a model of natural regulation (Caughley 1976), the Yellowstone natural regulation hypothesis, and a model of natural regulation that is less dependent on equilibrial assumptions.

Conclusion: Falsifiable hypotheses should be added to the list proposed by Houston (1976) to remove ambiguity. Hypothesized mechanisms of interaction between predators, prey, and plants should be quantitatively formulated (for example, through numerical simulation) so they are clearly stated and related to other ecological processes. Concepts of natural regulation should be refined to be consistent with current ecological knowledge. There should be a short-term evaluation of current understanding of population dynamics, the role of predation, and responses of plants to herbivory in recent and ongoing studies in Yellowstone.

Hypotheses: No hypotheses were tested or suggested.

Coughenour, M. B., and F. J. Singer. 1996a. Yellowstone elk population responses to fire - a comparison of landscape carrying capacity and spatial-dynamic ecosystem modeling approaches. Pages 169-179 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Climate

Category: Predictive model (4) - Gray literature

Purpose: To assess the effects of the 1988 fires on the "carrying capacity" of winter and summer elk ranges by linking a dynamic carrying capacity model with a geographic information system to calculate total energy and nitrogen transfer to the elk herd. The authors also evaluated the potential for using a more complex, spatially explicit ecosystem model.

Conclusion: Landscape carrying capacity and ecosystem modeling results both indicated that the winter 1988/89 die-off was mainly a result of the combined effects of drought and deep snow. The combined approach of landscape carrying capacity and spatially explicit ecosystem modeling provided quantitative and explanatory predictions, and identified important knowledge gaps. Spatial heterogeneity must be considered in any analysis, particularly the dynamic distributions of vegetation, snow and elk.

Hypotheses: No hypotheses were tested or suggested.

Coughenour, M. B., and F. J. Singer. 1996b. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573-593.

Topic(s): Climate, Competition, Human [anecdotal (6)], Aspen [anecdotal (6)], Willow [anecdotal (6)]

Category: Predictive model (4) - Journal article

Purpose: To investigate whether or not the northern Yellowstone elk herd has been limited by food and winter weather under the natural regulation policy. The authors examine elk population and distribution data collected on Yellowstone's northern winter range from 1969-1990, forage production and precipitation data from 1935-1988, and weather data from 1969-1990.

Conclusion: Management of elk in YNP has been controversial because there have been many conceptual models for elk population regulation. The northern Yellowstone elk herd is regulated through food limitation, and both density-independent fluctuations in total available forage and density-dependent fluctuations in the forage available to each elk.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Precipitation strongly affects summer calf recruitment and mortality.
2) Elk distribution and foraging are spatially constrained by deep snow.
3) Winter severity is more detrimental in late season than early, due to depleted energy reserves and poorer forage.
4) Early spring precipitation effectively lengthens the winter by restricting access to the summer range.
5) Less time on the summer range and lower energy reserves the following winter create a 1-year time lag between spring precipitation and adult mortality.

6) Although there is density-dependent competition for food, density-independent fluctuations in forage supply and forage availability prevent the population from attaining a static equilibrium.
7) Willow and aspen do not limit elk population size because elk abundance is regulated by herbaceous plants.
8) Winter stress has less of an effect on 6-8 month-old calves than on the smaller newborns in spring and summer due to poor nutrition of lactating females.

Coughenour, M. B., F. J. Singer, and J. Reardon. 1994. The Parker transects revisited: long term herbaceous vegetation trends on Yellowstone's northern winter range. Pages 73-95 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Grassland
Category: Experimental study (1) - Gray literature
Purpose: To reexamine the Parker transect results and compare with recent (1981-1989) efforts.
Conclusion: The original intent of the Parker transects were to monitor trends in range condition by detecting changes in relative species abundances and changes in total vegetated soil surface relative to nonvegetated soil surface. The Parker transects have provided data over a long period utilizing a consistent methodology. Nevertheless, their interpretability is reduced because the data are difficult to interpret, biologically and statistically. The authors recommend that YNP implement a program that institutes a wider diversity of plant-soil associations.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Competitive interactions between plant groups are altered by precipitation.
2) Changes in relative abundances of species and plant functional groups over time are the results of changing weather patterns over the period.
3) Elk grazing has not impaired plant growth on the northern winter range in spite of fluctuations in elk numbers.
4) Elk use the winter range during a time of year when most plants are dormant and after seasonal production has already occurred.

Crabtree, R.L., and J.W. Sheldon. 1999. Coyotes and canid coexistence in Yellowstone. Pages 127-164 *in* T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva, eds. *Carnivores in Ecosystems: the Yellowstone Experience.* Yale University Press, New Haven, Conn.

Topic(s): Predator
Category: Observational study w/o mechanistic explanation (3) - Book chapter
Purpose: To review the major ecological studies of the coyote and examine canid

coexistence and competition because it is the least understood and possibly the most important aspect of coyote ecology.

Conclusions: The authors discuss the ecology of the coyote from the ecosystem perspective, and with respect to competition with other canids. In YNP, coyotes kill more elk calves (neonates and older calves in the winter) than do grizzly bears and mountain lions combined. Prior to wolf reintroduction, coyotes killed an average 1,276 elk annually, the majority of which were neonates. An estimated 74% of the biomass intake during the 5 winter months came from elk (primarily carrion). Nearly, two-thirds of the live predation on elk involved old or starving individuals.

Hypotheses: No hypotheses were tested or suggested.

Creel, S., J.E. Fox, A. Hardy, J. Sands, B. Garrott, and R.O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814.

Topic(s): Human

Category: Observational study (3) – Journal article

Purpose: To assess the physiological stress responses of elk and wolves to snowmobile activity at three National Parks.

Conclusions: Although glucocorticoid concentrations of elk were higher in response to snowmobiles than to wheeled vehicles, no evidence was found that current levels of snowmobile activity are affecting the population dynamics of elk at YNP.

Hypothesis: The following hypothesis was tested:
Glucocorticoid levels of elk and wolves will be higher during periods of high snowmobile activity than at times when this activity does not occur. (SUPPORTED)
The following hypotheses/predictions were suggested:

1) Relatively stable population numbers and high fecundity of the elk in YNP during the past 35 years suggests that the fitness costs associated with prolonged exposure to snowmobile activity may be negligible.

DeByle, N.V. 1979. Potential effects of stable versus fluctuating elk populations in the aspen ecosystem. Pages 13-19 *in* M. Boyce and L. Hayden-Wing, editors. North American elk, ecology, behavior and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Aspen

Category: Literature review (5) - Book chapter

Purpose: To examine the potential for elk browsing to exterminate aspen in western Wyoming.

Conclusions: A rest-rotation grazing plan may allow a rest period for plant community recovery, remove selective pressure on preferred plant species, and prevent the least palatable plants from dominating.

Hypotheses: No hypotheses were tested or suggested.

DelGiudice, G. D., and F. J. Singer. 1996. Physiological responses of Yellowstone elk to winter nutritional restriction before and after the 1988 fires: a preliminary examination. Pages 133-135 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire
Category: Observational study w/o mechanistic explanation (3) - Gray literature
Purpose: To assess the nutritional restriction of elk on the Northern and Madison-Firehole Ranges from 1987 to1989.
Conclusions: Nutritional restriction was most severe in winter immediately following the fires of 1988-89, with recovery clearly evident by winter 1989-90. Nutritional stress was comparatively mild during the prefire winter of 1987-88.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) High U:C ratios during early winter may reduce elk survival and reproduction.

DelGuidice, G. D., U. S. Seal, and L. D. Mech. 1991. Indicators of severe undernutrition in urine of free-ranging elk during winter. Wildlife Society Bulletin 19:106-110.

Topic(s): Grassland
Category: Observational study (2) - Journal article
Purpose: To provide managers with reference values of urine characteristics for free-ranging elk and other ungulate species that indicate fat depletion and accelerated endogenous protein catabolism.
Conclusions: An elevated urea nitrogen:creatinine (U:C) ratio in snow-urine is a useful indicator of severe or prolonged undernutrition in elk. Elevated creatinine ratios of sodium, potassium and phosphorus may be used as supportive indicators.
Hypotheses: The following hypothesis was tested:
1) Urinary U:C may be used as an indicator of fat depletion and accelerated protein catabolism. (SUPPORTED)
The following hypothesis was suggested:
1) Most urine samples from winter-killed elk had U:C values greater than 24.0, these values may be used as an indicator of moribund elk.

Despain, D. G. 1996. The coincidence of elk migration and flowering of bluebunch wheatgrass. Pages 139-143 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. National Park Service Technical Report NPS/NRYELL/NRTR/96-01.

Topic(s): Grassland
Category: Experimental study (1) - Gray literature

Purpose: To determine if elk migration and bluebunch wheatgrass phenology are related in time.

Conclusions: Bluebunch wheatgrass flowered at the same time each year despite varying weather conditions. By the end of the growing season each year, the total green biomass outside exclosures equaled that inside exclosures. The maximum number of elk was counted during the preflower stage. Elk migration coincided with inflorescences being detected in the sheaths of the wheatgrass. The coincidence of elk migration and flowering of bluebunch wheatgrass could be entirely the vagaries of chance. More data is needed to obtain a more definitive answer.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Elk migration is related to the flowering of bluebunch wheatgrass.
2) The consistency with which bluebunch wheatgrass flowers indicates photoperiod control.
3) Forage quality may be a factor in the timing of Yellowstone elk migration.
4) The movement of cow and calf elk in spring was more related to the calving period than to plant development.

Despain, D. G., D. L. Clark, and J. J. Reardon. 1996. Simulation of crown fire effects on canopy seed bank in lodgepole pine. Pages 45-49 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Forest

Category: Observational study w/o mechanistic explanation (3) - Gray literature

Purpose: To determine the length of time lodgepole pine cones trees are subjected to flames during crown fire and the effect of that exposure on seed viability.

Conclusions: The crowns of canopy trees burned for an average of 24.5 seconds. There was no significant difference in burn time between single trees and stands. Unheated seed germination of serotinous cones was much lower than nonserotinous cones. Ten seconds of burning was enough to open all the cones. After nonserotinous germination declined, serotinous germination was stimulated.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Low seedling density after a burn and few cones remaining in burned crowns indicate a stand with a poor prefire cone crop.
2) Cones are subjected to more flaming needles than dry wood during crown fires.

Dobson, A., and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. Ecology 77:1026-1036.

Topic(s): Disease
Category: Literature review (5) - Journal article
Purpose: To outline the history and status of Brucellosis in Yellowstone bison and elk and propose a management plan for effectively controlling the spread to cattle.
Conclusions: Brucellosis transmission occurs by licking aborted fetuses and grazing contaminated forage. Less than 1% of Yellowstone elk tested positive for brucellosis suggesting that *Brucella* may not be endemic. Although the incidence of infection is low, there is a large population of elk on the Northern range; therefore elk are a threat to cattle as well as bison. Infected elk on the Northern Range are likely to acquire their infections from either bison or elk infected on the Wyoming feeding grounds, or when aggregated together in large herds in winter. The Yellowstone elk population would have to increase drastically, to sustain brucellosis at the high levels of prevalence exhibited in winter-fed elk in the National Elk Refuge. Serolgical tests developed for cattle are fairly unreliable for testing bison and elk, but tissue cultures are definitive. Removing animals without certainty of infection cannot certify a decreased level of infection in Yellowstone. The *Brucella* vaccine available for cattle has been used with limited success for elk and marginally for bison. Recommendation for a buffer zone around the park is presented as a viable solution for cattle safeguarding based on statistical projections of infected Yellowstone populations and feasibility.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Slightly more than 50% of Yellowstone bison need to be inoculated to eradicate brucellosis in YNP.
2) Cattle can be safeguarded from infected Yellowstone ungulates by creating a buffer zone around the park for wandering Yellowstone animals in winter.

Ellis, M., C.D. Von Dohlen, J.E. Anderson, and W.H. Romme. 1994. Some important factors affecting density of lodgepole pine seedlings following the 1988 Yellowstone fires. Pages 139-150 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Forest, Fire, Aspen
Category: Experimental study (1) – Gray literature
Purpose: To investigate how fire severity and pre-fire stand composition interact to control the regeneration of lodgepole pine.
Conclusions: Seedling density was higher in moderately burned than severely burned transects. Other conifer species were infrequent in all study areas. Aspen seedlings were present in moderately burned and canopy burn areas. The number of lodgepole pine cones on the ground in 1990 was consistently

higher in moderately burned areas and positively correlated with seedling density. Regardless of burn severity, lodgepole pine seedling density was only weakly correlated with cones remaining in the crowns of dominant trees. Seedling densities in remote, severely burned transects were greatly reduced compared with canopy-burned transects adjacent to a seed source. Pre-fire serotiny across sites was generally low, though the incidence of serotiny was quite variable even over short distances. Post-fire lodgepole pine seedling density is a function of pre-fire serotiny. Pre-fire stand densities and ages are markedly similar among transects within any given site.

Hypotheses: The following hypotheses were tested:

1) Seedling density is higher in areas subjected to fire of moderate intensity than in adjacent areas subjected to severe canopy fire. (SUPPORTED)
2) An inverse relationship exists between seedling density in areas of severe canopy fires and distance to the nearest moderately burned or unburned stand serving as a seed crop source. (SUPPORTED)
3) A stand's pre-fire level of cone serotiny will determine seed availability. (SUPPORTED)
4) Local differences in burn severity result from stochastic factors (e.g., wind) rather than local differences in stand structure. (SUPPORTED)

The following hypotheses / predictions were suggested:

1) Differences in seedling densities between moderately and severely burned transects result from differential seed mortality caused by local fire intensity.
2) The serotiny mosaic is related to burn severity in much the same way as seedling densities.
3) Severely burned areas with extremely low initial seedling densities will develop into open grown stands containing few dominant individuals that will slowly fill in gaps and produce a mixed age stand.
4) The majority of the park's burn areas will be characterized by extensive even-aged forests.
5) "Dog-hair" stands of lodgepole pine are more likely to occur in areas subjected to moderate than severe fires.

Farnes, P. E. 1996. Impact of 1988 Yellowstone fires on snowmelt water yields. Pages 39-42 135 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Forest
Category: Anecdotal (6) - Gray literature
Purpose: To evaluate methods for predicting increases in water yields resulting from alteration of forest canopy whether by fire, insects, or logging.

Conclusions: The analytical estimates of spring runoff resulting from the 1988 fires were between 2.7 and 4.3 for the Yellowstone River at Corwin Springs and 5.9 to 7.6 percent for the Madison River near Grayling. Actual run off has been 2.7% greater for the Yellowstone and 5.9% greater than predicted for Grayling. A longer evaluation period is recommended before revision of predicting procedures and equations.

Hypotheses: No hypotheses were tested or suggested.

Ferrari, M.J., and R.A. Garrott. 2002. Bison and elk: brucellosis seroprevalence on a shared winter range. Journal of Wildlife Management 66:1246-1254.

Topic(s): Competition, Disease, Fire [anecdotal (6)], Geothermal [anecdotal (6)], Forest [anecdotal (6)], Topography [anecdotal (6)]

Category: Observational study (2) – Journal article

Purpose: To address concerns that increasing numbers of bison and subsequent changes in their winter distribution in YNP will lead to increased range overlap with elk and higher interspecific transmission rates of brucellosis between these two species.

Conclusions: Elk winter range spanned across wide topographical gradients and elevations and encompassed geothermal areas, but was primarily composed of burned forest habitat. Conditions in the Madison-Firehole winter range promote a high degree of overlap between bison and elk (53-76%). Elk winter range used by bison was confined to lower elevation, flat meadow communities along river corridors. Despite high levels of commingling between elk and bison on winter range, the 3% seroprevalence rate in the Madison elk herd suggests that interspecies transmission of brucellosis from bison to elk in the Madison-Firehole area is low and comparable to populations of elk that do not interact with bison.

Hypotheses: The following hypotheses were tested:
The energetic and foraging benefits to bison and elk provided by the thermal and river systems in YNP will result in a decrease in ecological separation. (SUPPORTED)
2) Decreased ecological separation of bison and elk at times of the year when brucellosis transmission is possible will lead to increased exposure to *B. abortus* in local elk populations relative to those in other regions. (REJECT)
The following hypotheses/predictions were suggested:
1) The low incidence of interspecies transmission of brucellosis between elk and bison may be the result of lower levels of active *B. abortus* infection in bison than is suggested by the seroprevalence rate, shedding of low numbers of *B. abortus* by infected animals, a short interval of viability of *B. abortus* outside the host, ingestion of insufficient quantities of bacteria to constitute an effective dose, or a combination of these.
2) The wide distribution of geothermal activity across the Madison-Firehole may result in less aggregation of animals in the winter than those

populations found in areas where supplemental feeding occurs, thus potentially increasing disease transmission in the later type of area.

Fowler, C.W., and W.J. Barmore. 1979. A population model of the northern Yellowstone elk herd. Pages 427-434 *in* R.M. Linn, editor. Proceedings of the First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, November 9-12, 1976. National Park Service, USA.

Topic(s): Predators
Category: Predictive model (4) - Gray literature
Purpose: To incorporate existing data from 1935-1975 into a model that can be used to estimate the carrying capacity for elk on the northern range, and to examine the possible effects of predation on the population
Conclusions: A model was developed to estimate the carrying capacity for elk on the northern range. Carrying capacity is defined as the number of elk in a population when the mean rate of change is zero. The model is derived from data collected during a period when hunting occurred, but there were no wolves in the ecosystem. The authors conclude that predation could influence the size of the northern range elk herd.
Hypotheses: No hypotheses were tested. However, the following hypothesis was suggested:
1) The synergistic effect of predation and hunting may reduce elk populations to levels considerably below those that would result from either factor acting in absence of the other.

Frank, D. A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. Wildlife Society Bulletin 26:410-418.

Topic(s): Grassland
Category: Observational study (2) - Journal article
Purpose: To investigate the indirect effects of herbivory on ecosystems that feedback on ungulates themselves.
Conclusions: Animals grazed young nutritionally rich forage as they migrated through spring and summer. Herbivores grazed patches in the landscape according to forage availability, and the intensity of grazing increased as plant production increased. Grazers increased aboveground plant production by an average of 45% indicating a significant positive feedback. Results indicate a two fold increase in net N mineralization of grazed verses fenced areas. Seasonal migration is a critical component in both of these feedbacks, allowing grazed vegetation an extended rest period for regrowth. Grazed sites ranged fourfold in soil moisture, and more than 10 fold in C and N, yet in contrast herbivores had no effect on soil properties.
Hypotheses: No hypotheses were tested or suggested.

Frank, D. A., and P. M. Groffman. 1998. Ungulate versus landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Topic(s): Grassland, Topography
Category: Experimental study (1) - Journal article
Purpose: To examine how herbivores and landscape factors affect soil C and N dynamics in Yellowstone National Park grasslands and how these factors effect N mineralization and soil organic matter quality.
Conclusions: The regulatory influences of herbivores on soil N may be more significant than previously suspected. Despite a fourfold variation in average growing season soil moisture and a >10 fold increase in soil C and N content across sites, we found that grazers had an additional twofold enhancement on N cycling and dramatically increased between site variation. Ungulates had no influence on any measured soil property except soil moisture. Laboratory studies support the notion that herbivores improve organic matter quality, but this change was not reflected in a change in soil C/N ratios. This suggests that the entire C/N ratio may not reflect turnover in the field. Moisture was not involved in stimulation of N cycling because grazed soils were drier than fenced. A reduction in N immobilization played a role in ungulate stimulation of net N mineralization in Yellowstone. Soil C content and C/N ratios did not differ between grazed and 33-37 year-old ungrazed areas, which suggests the mechanisms for grazer-induced increases in N mineralization differ from those proposed in mixed grass prairie studies (Holland and Detling 1990, Holland et al. 1992). Soil beneath shrubs had higher moisture content than grassland interspaces, but soil C and N did not differ.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Ligin content may be important in controlling turnover rates of grassland soil organic matter.
2) Herbivores may promote soil N cycling by changing soil temperature and/or moisture regimes.
3) The effect of shrubs on mineral cycling may vary among grasslands and not always increase nutrient pools and flows, as has been indicated by previous work.

Frank, D. A., and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. Oikos 62:360-362.

Topic(s): Grassland, Climate
Category: Experimental study (1) - Journal article
Purpose: To examine the effect of a severe regional drought on plant species composition on the Northern Range
Conclusions: Resistance of community species to change was positively correlated with species diversity. Stability increased as a result of microsite dissimilarities of species composition rather than microsite richness. Similar responses of

grazed and ungrazed samples indicate a dominant role of weather. No other variable measured (elevation, primary production, soil capacity for holding water, or bulk density) could be correlated with resistance of species composition to change. The number of species affected by drought did not change as grassland resistance increased, even though species richness increased.

Hypotheses: The following hypothesis was tested:
1) Stability of plant species composition increases with diversity. (SUPPORTED)
The following hypothesis was suggested:
1) Increased plant community heterogeneity increases community resistance to perturbations.
2) An increase in pattern diversity with species diversity may reflect enhanced species compartmentalization resulting in declines in species interactions.
3) Pattern diversity can facilitate community stability to severe climatic changes.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores and drought in Yellowstone National Park. Ecology 73:2043-2058.

Topic(s): Grassland, Topography [observational study (2)]
Category: Experimental study (1) - Journal article
Purpose: To examine the effect of abundant native large herbivores on ecosystem function of a spatially and temporally heterogeneous temperate grassland.
Conclusions: Plant growth occurs locally as a brief strong pulse and regionally as a landscape wave. Nitrogen content of dominant grasses was highest just after snow melt and declined through the growing season. Because N content and green biomass concentration are highest during plant growth, ungulates prolong a nutritionally rich diet by following the wave of plant growth up the elevational gradients, thereby maintaining high foraging efficiency. Plant communities that were quasi-monocultures were not grazed, but ungulates grazed in areas adjacent to them. There is a positive spatial association between aboveground production and consumption, and consumption and nutrient return to the site. Herbaceous production, dung deposition, and nutrient fluxes declined at nearly all sites from 1988 to 1989 when there were fewer grazers in the system. Direct effects on ungulate consumption and indirect effects through wildfire were likely involved in the decline of elk and bison numbers.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Monoculture communities of plants that are not grazed are avoided due to low forage quality or low palatability.

Frank, D., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157-161.

Topic(s): Grassland, Topography [observational study (2)]
Category: Experimental study (1) - Journal article
Purpose: To provide evidence that elk and bison stimulate grassland production and examine spatio-temporal patterns of grazing.
Conclusions: Production of grazed areas was significantly higher than fenced areas. Native large herbivores promote aboveground grassland production in Yellowstone.
Hypotheses: The following hypothesis was tested:
1) Stimulation of aboveground production by ungulates may be due to the migratory behavior of native ungulates that track young, high quality forage as it shifts across the Yellowstone landscape. (SUPPORTED)
The following hypothesis was suggested:
1) Sites that are only grazed in winter must have productivity stimulated by mechanisms other than plant regrowth after defoliation (i.e. fertilization or standing dead removal).

Frank, D. A., and S. J. McNaughton. 1994. Plant-ungulate ecology of grasslands on the northern range of Yellowstone National Park. Page 317 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Grassland
Category: Experimental study (1) - Gray literature
Purpose: To determine the effect of ungulates on above-ground production of the Northern Range and measure plant production and herbivore consumption.
Conclusions: An average of 45% of above-ground productivity was consumed among grazed sites. Above ground production had a positive linear relationship with amounts consumed by ungulates. Consumption of plants occurred while plants were still growing. Young vegetation had a higher nitrogen content than phenologically older tissue; therefore ungulates increased their use of a high quality diet by tracking young vegetation across the landscape.
Hypotheses: No hypotheses were tested or suggested.

Frank, D.F., M.M. Kuns, and D.R. Guido. 2002. Consumer control of grassland plant production. Ecology 83:602-606.

Topic(s): Grassland
Category: Experimental Study (1) – Journal Article
Purpose: To examine the effects of large herds of migratory ungulates on ecosystem primary production comparing above ground (NAP) and below ground

production (NBP) in grazed and ungrazed (fenced) grassland in nine widely variable grasslands

Conclusions: The results of this study indicate that the predominant effect of grazers on grasslands was a facilitating influence on the below ground food web. Although climate, e.g., temperature and precipitation, and mineral soil parent material are known as the major determinants of primary productivity results for grazed grasslands in Yellowstone Park indicate that consumers also exert strong top-down control over ecosystems primary production. The result that grazers enhance root mortality provides a mechanistic explanation for herbivores increasing soil organic matter and rates of nutrient turnover in Yellowstone grassland. Moreover, these findings indicate that grazing does not necessarily reduce carbon flow to soil and thereby provide a potential explanation for the genesis of C-rich soils that they likely experienced chronic herbivory through out their development.

Hypotheses: The following hypotheses were tested:

1) Herbivory facilitated primary production of Yellowstone Park grasslands (SUPPORTED)
2) Grazer facilitation of NAP is positively related to herbivore consumption (SUPPORTED)
3) Grazer facilitaion of NAP is positively related to herbivore grazing intensity (SUPPORTED)
4) Grazer facilitation of NBP and whole plant productivity (NPP) is positively related to either herbivore consumption, herbivore grazing intensity or both (WEAKLY SUPPORTED)

The following hypothesis/prediction was suggested:

1) Migratory behavior of Yellowstone ungulates provides grazed plants with sufficient time to recover and, therefore may be an important property of this ecosystem

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26:163-188.

Topic(s): Grassland, Climate [anecdotal (6)], Topography [observational study (2)]

Category: Experimental study (1) - Journal article

Purpose: To examine nitrogen dynamics of a grazed watershed in Yellowstone and to compare N mineralization rates with those reported for other semi-arid grassland and shrub-grassland ecosystems.

Conclusions: Grassland bench sites had higher soil N and C levels than the ridgetop and slope sites. High mineralization rates during spring were coincident with intense grazing before ungulates migrated to higher elevations. The average annual rate of N excreted from ungulates was 27% of the annual N mineralized, which is 4.5 times higher than the N in senescent plant tissue. N in the soil from ungulates and plant tissue accounted for only 33% of the total N mineralized. The annual rate of N mineralization in Yellowstone was

higher than that of other western grassland systems. There was higher N availability at the riparian site than grassland sites, yet the riparian site had the lowest rate of mineralization. Most of this N accumulated in resin during peak snow melt when the riparian site was flooded. When patches of the riparian zone were fertilized, above ground production was stimulated indicating that the zone was N-limited

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Variation in climate may produce significant inter-annual variability in N mineralization in this grassland ecosystem.
2) There is a net movement of N over the year from high elevation summer range, where ungulates gain body mass, to winter range, where body mass is lost.
3) Other animals, including pocket gophers, ground squirrels, voles, and grasshoppers may be significant contributors of N for microbes.
4) N_2 fixation by cynobacteria may be an important N source in Yellowstone grassland.
5) Ammonia volatilization and denitrification rates may be particularly important pathways for N loss on the Northern Range.
6) The riparian zone in this watershed is not a passive conduit through which nutrients move, but is biologically responded to biogeochemical processes occurring upslope and upstream from it.

Frank, D., S. J. McNaughton, and B. F. Tracey. 1998. The ecology of earth's grazing ecosystems. Bioscience 48:513-521.

Topic(s): Grassland
Category: Literature review (5) - Journal article
Purpose: To review the functional similarities between Yellowstone and Serengeti grasslands and comment on ungulate-facilitated nutrient flows in these systems.
Conclusions: Yellowstone and the Serengeti are "grazing ecosystems" and are distinguished from other habitats by herbivore-based food webs and the extent that ecological processes are regulated within that food web. Grazers increase biomass productivity and contribute to indirect effects that increasing nitrogen mineralization and other geochemical processes. A continuum among grazing ecosystems exists from relatively less productive and moderately grazed temperate grassland to a highly productive and heavily grazed tropic grasslands. Feedbacks effects are stronger in the Serengeti and grazers have a larger effect on primary production. Grazing systems have historically been transformed into pasture and open ranges supporting domesticated animals and food-producing regions for cultivation. These systems are critically endangered terrestrial habitats.
Hypotheses: No hypotheses were tested or suggested.

French, S.P., and M.G. French. 1990. Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986-88. International Conference on Bear Research and Management 8:335-341.

Topic(s): Predator
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To investigate the predatory behavior of grizzly bears feeding on newborn elk calves.

Conclusions: One third of the predatory behavior events documented involved sows and young. Some grizzlies were deliberate predators and effectively preyed on newborn elk calves for short periods in each spring. Bedded calves were hunted more frequently than active calves. Sight was vital in all aspects of hunts, including the stalk and selection. Adult elk successfully defended calves by running between the bear and calf. There was uneven use of elk calves among various age classes of grizzly because adult males were preoccupied with courting and mating during elk calving season.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Acquisition of predatory skills for preying effectively on calves is facilitated when cubs are raised and taught by mothers.
2) Some grizzlies are excluded entirely from elk calving grounds by dominant bears.

French, M. G., and S. P. French. 1996. Large mammal mortality in the 1988 Yellowstone fires. Pages 113-115 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire
Category: Observational study w/o mechanistic explanation (3) - Gray literature
Purpose: To document large animal behavior and mortality in relation to fire.
Conclusions: Large animals were not observed fleeing a fire front and most animals appeared indifferent even when fires were nearby. Although 333 elk in Yellowstone and surrounding forests were killed in the 1988 fires, this only represented less than one percent of the population. Most animals died of smoke inhalation before arrival of the fire front.
Hypotheses: No hypotheses were tested or suggested.

Garrott, R.A., L.L. Eberhardt , J.K. Otton, P.J. White, and M.A. Chaffee. 2002. A chemical trophic cascade in Yellowstone's geothermal environments. Ecosystems 5:659-666.

Topic(s): Geothermal, Parent material, Predation
Category: Observational Study (2) – Journal article

Purpose: To contrast the differences in two Yellowstone Park locations (Lamar Valley and Madison River drainage) for rock, stream sediment, and water chemistry, and of geothermal heat, and trace of ecological consequences of these differences through the plant- herbivore-carnivore trophic chain

Conclusions: Fluoride (F) and Silica (SiO_2) are enriched in virtually all the waters of the Madison River drainage. The fluoride and silica chemistry of stream water and stream sediment is closely related to a combination of the chemistry of exposed rock material and that of chemical additions caused by geothermal activity. Plants growing in the Madison River drainage contained higher levels of F, and in some environments, higher SiO_2, than plants collected at similar sites in the Lamar River drainage. Elk mandibles collected in the Madison drainage basin contained approximately sixfold higher levels of F than those collected from northern range elk, demonstrating classic signs of fluoride toxicosis. The compromised dentition of elk living kin the Madison drainage basin is responsible for a dramatically abbreviated survival schedule with those of the Lamar River Valley. Because wolves preferentially prey on the young of the year and senescent animals, the geothermally induced altered age structure of the Madison drainage elk population results in a higher proportion of the adult population being susceptible to wolf predation.

Hypotheses: The following hypotheses were tested:

1) Fluoride and Silica concentrations are higher in the Madison River drainage than Lamar valley. (SUPPORTED)
2) Plants collected in the Madison River drainage are higher in Fluorine and Silica than plants collected in similar sites in Lamar Valley (SUPPORTED)
3) Elk tend to concentrate in thermal refugia as snowpack increases (SUPPORTED)
4) Elk mandibles collected in the Madison River drainage contain higher concentrations of fluorine compared with mandibles collected in the Lamar Valley (SUPPORTED)
5) Elk age specific survival will be lower in the Madison River drainage than Lamar Valley (SUPPORTED)

The following hypotheses/predictions were suggested

1) Because wolves preferentially prey on the young of the year and senescent animals, the geothermally induced altered age structure of the Madison drainage elk population results in a higher proportion of the adult population being susceptible to wolf predation.
2) The ability of the elk herd to demographically compensate for wolf predation will be limited by a reduced population growth rate because of early senescence.

Gese, E.M. 1998. Threat of predation: do ungulates behave aggressively towards different members of a coyote pack? Canadian Journal of Zoology 77:499-503.

Topic(s): Predator
Category: Observational study (2) - Journal article
Purpose: To answer questions relating to seasonal patterns of aggression by ungulates towards coyotes, male versus female ungulate aggression frequencies, possible relationships between displays of aggression by an ungulate and the size of a coyote group, and if ungulates perceive and direct aggression towards potential leaders of an attack before an attack happens.
Conclusions: Adult ungulates initiated a chase or attack on alpha coyotes more frequently than expected. Beta coyotes and pups were chased less frequently. Ungulates directed aggression towards larger individuals that had the greatest tendency to initiate attacks. The highest rate of ungulate aggressive behavior occurred during fawning and calving season. Aggression declined through autumn and winter. Female ungulates initiated most attacks and chases during the summer.
Hypotheses: The following hypothesis was tested:
1) Ungulates choose the largest coyote to attack. (SUPPORTED)
The following hypothesis was suggested:
1) Alpha coyotes may display subtle behaviors or postures that are indicative of hunting and serve as cues for ungulates, but are undetectable by humans.

Gese, E.M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist 133:36-43.

Topic(s): Predator
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To provide insight into the roles assumed by members of coyote packs when cooperatively hunting large prey and the ecological conditions under which coyotes can succeed.
Conclusions: The alpha male was the main aggressor in cooperative kills, even when other pack members were present. Elk that retreated into the water before coyote pursuit were not attacked. Snow depth influenced the success of winter attacks on elk and deer. In three kills, coyotes were able to walk on the snow crust, whereas the elk punched through. Five kills involved lone elk; in 2 of 4 unsuccessful attempts, the attacked elk was with another herd member.
Hypotheses: No hypotheses were tested. However, the following hypothesis was suggested:
1) The coyote's smaller body size and dependence on small prey throughout the year has precluded them from evolving a fully cooperative system of hunting.

Green, G. I., D. J. Mattson, and J. M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. Journal of Wildlife Management 61:1040-1055.

Topic(s): Predator, Geothermal, Topography, Human
Category: Observational study (2) - Journal article
Purpose: To describe predator selectivity with respect to species, sex, and age class of the carcass, and whether selectivity varied by winter range, abundance of carrion, cover, and human facilities.
Conclusions: Grizzly bears used bison carcasses more frequently than elk carcasses. Smaller elk carcasses were not used. The likelihood that a grizzly used an ungulate carcass during spring increased with elevation. Grizzlies underused carcasses within 400 meters of roads and within 5 km of major recreational developments. Geothermally-influenced areas with high concentrations of ungulates are important areas for grizzly bears owing to the prevalence of ungulate carcasses.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Wolves may cause changes in ungulate herd composition and increase abundance of ungulate carcasses on winter ranges.
2) Without preservation of carcasses in peat and water, small carcasses would not be available to bears.
3) Geothermal areas often coincide with heavy human activity and reduce grizzly use of carrion.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713.

Topic(s): Grassland, Fire
Category: Literature review (5) - Journal article
Purpose: To review research on the indirect effects of ungulates on the environment.
Conclusions: Ungulates modify nutrient cycling, influence primary production, alter patch dynamics, and affect abiotic disturbances. They regulate process rates, modify spatial mosaics, and control transitions between alternative ecosystems. Volatile compounds in woody material deter herbivory and benefit these plants. This may lead to an increased likelihood of crown fire.
Hypotheses: No hypotheses were tested or suggested.

Houston, D. B. 1976. Research on ungulates in northern Yellowstone National Park. Pages 11-27 *in* R. Linn, editor. Research in the parks, transactions of the National Park Centennial Symposium. USDI NPS Symposium Series Number 1, U.S. Government Printing Office, Washington, D.C. USA.

Topic(s): Grassland, Human, Willow, Competition
Category: Literature review (5) - Journal article

Purpose: To review the approach to research on Yellowstone's ecosystems and evaluate posed hypotheses.

Conclusions: Historical accounts do not support the reports of an elk population eruption and crash in the early 1900s. The 'reported' population eruption is the result of a changing definition of the northern herd which has included counts of elk wintering in the Gallatin, Madison, Firehole, and Shoshone Rivers, in addition to the Yellowstone and Lamar Rivers. Misinterpretations of discrepancies between counts and calculations account for reported population surges and crashes. Mapped distribution of ridgetop sites with plant communities showing 60% or more bareground and historical photos, revealed that zootic communities are underestimated and reports of overgrazed communities are overestimated. Willow has declined in the park and outside the park. Willow has also persisted on, and colonized, pioneer substrates in the northern range in the presence of wintering ungulates. It is too early to claim conclusive support for most hypotheses.

Hypotheses: The following hypotheses were tested:
1) Low densities of herbaceous vegetation on certain ridgetop sites represent naturally occurring zootic climax vegetation, not retrogressive plant succession. (SUPPORTED)
2) Replacement of willow and aspen communities in the winter range does not represent retrogressive succession, but indicates primary and secondary succession. (SUPPORTED)
The following hypotheses were suggested:
1) Density, composition, and successional trends of vegetation will not depart from natural conditions as a result of natural regulation.
2) Public hunting will not result in a conditioned avoidance behavior among elk causing an unnatural concentration of elk in the park.
3) Natural regulation or effects of hunting outside the park will not result in competitive exclusion of sympatric herbivore species because of interspecific competition.
4) Changes in willow represent primary succession which reflect some fundamental change in hydrology and alluviation on streams.
5) Climatic changes dating from the Gannett Peak Stage of neoglaciation may explain vegetation changes in Yellowstone.
6) The high densities of big sage at this low elevation represented a disclimax community that resulted primarily from grazing by domestic livestock. The observed decline in big sagebrush as result of native grazers represents a return to more natural conditions.

Houston, D.B. 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. Journal of Applied Ecology 15:653-661.

Topic(s): Human, Predator, Disease

Category: Observational study w/o mechanistic explanation (3) - Journal article

Purpose: To (1) evaluate elk as a food source for predators and scavengers, (2) make indirect inferences about the abundance of these secondary consumers, and (3)

examine the role of ungulate mortality in relation to the park's primary purpose of maintaining a representative natural ecosystem.

Conclusions: No animal was considered to have died of starvation, but most deaths seemingly involved the interaction of disease, parasites, and predators on young and old animals. Estimates of elk mortality are deliberately conservative. Unusually large proportions of uneaten carcasses are found along roadsides. In some small areas the carrion exceeded what carnivores could eat, and coyotes, ravens, and bears were still feeding on carcasses in mid-June. Partly consumed carcasses or unconsumed carcasses were exploited by large populations of insect larvae, which in turn, attracted insectivorous birds. Bears also fed on larvae illustrating the complexity of food web relationships. The mortality of the elk should not be considered a waste in terms of elk management.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Wolf populations might substitute for, or add to, other agents and change the timing of some elk mortality.

Houston, D.B. 1979. The northern Yellowstone elk – winter distribution and management. Pages 263-272 *in* M. Boyce and L. Hayden-Wing, editors. North American elk, ecology, behavior and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Grassland, Predator, Human

Category: Predictive model (4) - Book chapter

Purpose: To review hypotheses posed by other researchers during 1968-1978 concerning elk distribution and management.

Conclusions: Previous hypotheses assumed that hunting removals would be similar to those from 1935-1956. The population of elk at the time of this study reached the highest estimates of carrying capacity, and the author recommends monitoring the trend of growth to substantiate or reject any predictions. The author recommends that if elk population reduction is resumed in the park, then elk that do not migrate out of the park should be the last selected because they are valuable food for predators. The ability to restore migration patterns outside the park is supported by the last 11 years of data. The hypothesis that hunting outside the park could be conducted without causing artificial concentrations of elk in the park is rejected based on attempts in 1976 and 1978. A reasonable settlement needs to be designed to allow for lower elk densities outside the park to protect agricultural resources, private property from damage, and still allow recreational hunting.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) The frequency of migrations and numbers of elk moving outside the park during winter will increase at higher overall densities in the park.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17-29.

Topic(s): Grassland, Willow, Aspen, Human, Beaver, Topography, Predator, Fire

Category: Anecdotal (6) - Journal article

Purpose: To review research on Yellowstone ecosystem processes and to discuss the historical, scientific, and social controversy regarding natural regulation.

Conclusions: Erosion in YNP park is not a result of overgrazing and shows no difference from long-standing erosion patterns found in drainages. Most erosion leading to sediment loads on the Yellowstone and Lamar Rivers comes from steep, high elevation areas that are uninhabited by elk. As elk and bison follow vegetation phenology across the landscape, the species not only optimize the nutritional quality of their diet, but through their movements, urine and feces, tilling the soil through hoof action, and herbivory, they promote dense short grass stands and stimulate above ground growth. Higher native plant diversity occurs on grazed sites. Elk are a contributing factor in aspen demography, but they are not the only factor. Willow has not declined since the late 1950s. Prehistoric descriptions of the area confirm that vertebrate species with few exceptions have persisted in Yellowstone for at least 3200 years. Native Americans used fire and burned grasslands and warrant historical investigation. Despite the importance of hunting on elk populations, severe winter weather is the most significant of all mortality factors. Calf winter survival is inversely related to elk population size. Predators kill one third of all new calves before they are a month old. Other ungulate populations are unlikely to compete with elk for resources, and many species have increased in population size. There is little question that beaver populations were much higher in 1872, but there are explanations that involve more than elk population size. Many critical questions remain unanswered and thresholds indicating the need for intervention or research need to be established.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Ungulates will destabilize streambanks and limit or eliminate riparian vegetation.

2) Riparian woody communities are declining.

3) Ungulates contributed to limited aspen growth before 1872.

4) Elk select against previously browsed aspen clones in subsequent years due to differences in palatability.

5) Elk did not return in subsequent years to the same aspen clones due to severe drought conditions.

6) Aspen clones escape height inhibitive browsing by growing beyond elk reach before being exploited again.

Jackson, S. G. 1993. The effect of browsing on bird communities. Utah Birds 9:53-63.

Topic(s): Willow, Aspen
Category: Literature review (5) - Journal article
Purpose: To examine the potential effects of browsing on bird communities
Conclusion: If browsing pressure is high enough, vegetational changes may be severe enough to adversely affect songbirds. Moderately browsed stands had a more heterogeneous mixture of tall and short willows, and more complex vegetation structure involving open patches and corridors among clumps of willows.
Hypotheses: The following hypothesis was tested:
1) Intense browsing by ungulates has a negative effect on songbirds. (SUPPORTED).
No additional hypotheses were suggested.

Jakubas, W.J., R.A. Garrott, P.J. White, and D.R. Mertens. 1994. Fire-induced changes in in the nutritional quality of lodgepole pine bark. Journal of Wildlife Management 58:35-46.

Topic(s): Fire, Forest
Category: Experimental study (1) – Journal article
Purpose(s): To determine whether the 1988 fires improved the overall nutritional quality of lodgepole pine by altering the chemical composition and digestibility of the bark. To comparatively assess the nutrition of burned lodgepole pine bark to other winter forages used by elk.
Conclusions: Burned lodgepole pine bark was more digestible and contained more crude protein and less secondary metabolites than that of unburned trees. Burned bark of lodgepole pine, however, is lower in nutritional quality compared to other winter forages.
Hypotheses: The following hypothesis was tested:
1) Burned lodgepole pine bark is higher in nutritional quality than unburned pine bark. (SUPPORTED)
The following hypotheses/predictions were suggested:
1) Consumption of burned lodgepole pine bark by elk may be more related to the efficiency of with which they can obtain bark than to its nutritional quality.
2) Decreased levels of secondary metabolites in the bark of burned lodgepole pine versus unburned bark may lead to increased herbivory of the former.

Kay, C. E. 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. Pages 131-160 in G. W. Workman, editor. Western elk management: a symposium. Utah State University, Logan, Utah, USA.

Topic(s): Aspen, Human, Fire, Climate, Willow [anecdotal (6)]

Category: Observational study (2) - Gray literature
Purpose: To determine if aspen reproduction varied by location both inside and outside Yellowstone National Park and to determine the probable successional status of these aspen stands based on the presence or absence of conifers in the understory.
Conclusion: The 799 aspen stands that were measured inside YNP had an aspen regeneration rate of 4%, while 3,082 stands outside the park had an aspen reproduction rate of 60%. This difference was due primarily to repeated browsing by elk that are protected in the Park, and not due to differences in climate or fire suppression. The decline of willow is also likely the result of elk browsing. Yellowstone should not be cited as an example of successful natural regulation.
Hypotheses: The following hypotheses were tested:
1) Intense browsing by ungulates prevents aspens from growing into mature trees, and is responsible for aspen decline in YNP. (SUPPORTED)
2) Aspen is a seral species maintained by fire, and human suppression of natural fires is primarily responsible for the observed aspen decline in YNP. (REJECTED)
3) If natural regulation is occurring, native ungulate populations will naturally stabilize without causing retrogressive plant succession. (REJECTED)
No additional hypotheses were suggested.

Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. Northwest Science 67:94-104.

Topic(s): Fire, Aspen
Category: Anecdotal (6) - Journal article
Purpose: To document and report aspen seedling establishment following wildfires.
Conclusion: Newly established vegetation in burned areas had an average canopy cover of 12%. Bare mineral soil was often exposed in these burned areas. All of the aspen seedlings observed in Grand Teton National Park and YNP were associated with bare mineral soil, ash, and an absence of competing vegetation following wildfires. From 1989 to 1991, average height of the aspen seedlings declined from 58 cm to 47 cm. By 1991, all aspen seedlings showed signs of repeated ungulate winter browsing.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Ash from forest fires may promote aspen seed germination and survival.
2) Elk may prevent aspen seedling height growth and their development into trees.
3) The high level of ungulate use in YNP may prevent aspen seedlings from growing into mature trees.
4) Catastrophic fires may be important in the establishment of aspen from seed.

Kay, C. E. 1997. Yellowstone: ecological malpractice. PERC Reports 15:3-39.

Topic(s): Willow, Aspen, Beaver, Predator, Human, Climate
Category: Anecdotal (6) - Gray literature
Purpose: To provide evidence that the current management philosophy of natural regulation at YNP is not working and must be rejected.
Conclusion: Historical evidence suggests that Native Americans kept ungulate numbers low, thus promoting the occurrence of high plant and animal diversity. Over-abundant elk have destroyed the park's willow and aspen communities. Tall willows can be found outside the park where elk numbers are lower. The climate inside and outside the park is similar, therefore the decline of willow is not climate-related. Willows inside exclosures are taller, provide a denser canopy cover, and produce abundant seed compared to willows outside exclosures. Beaver were once common in YNP, but overbrowsing of aspen, willow, and cottonwood by elk has resulted in beaver decline. Without beaver, streams have been down-cutting, the water table is lowered, and riparian vegetation has been lost. Overabundant ungulate populations inside YNP have destroyed the vegetation that grizzly bears rely upon for food. Bears are forced to leave the park in search of food where they often are killed by humans.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Burning plus repeated browsing hastens the elimination of aspen.
2) Aspen supports the highest biodiversity of any forest type in YNP.
3) Elk herbivory has prevented aspen growth and eliminated aspen from much of YNP.
4) Elk have caused the decline and ecological extinction of beaver in YNP.
5) Over-abundant elk have had negative impacts on Yellowstone grizzly bears.

Kay, C. E. 1998. Are ecosystems structured from the top-down or bottom-up: a new look at an old debate. Wildlife Society Bulletin 26:484-498.

Topic(s): Human, Aspen
Category: Literature review (5) - Journal article
Purpose: To provide a review of the evidence that Native Americans were once the ultimate keystone species, creating the ecosystems that we now consider "natural".
Conclusion: The number of elk in modern YNP is not characteristic of what occurred in the Park prior to the arrival of Europeans. Native Americans suppressed ungulate populations during pre-Columbian times. Historical photographs indicate higher aspen, willow, cottonwood, and beaver densities, and suggest a high use of berries by aborigines. Predation by aboriginal

people, not food, limited ungulate populations. Until the importance of aboriginal land management is recognized and modern management practices are changed accordingly, YNP will continue to lose biological diversity and ecological integrity.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Native Americans kept ungulate populations suppressed during pre-Columbian times

Kay, C. E., and S. Chadde. 1991. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. Proceedings: Symposium on Ecology and Management of Riparian Shrub Communities. Intermountain Research Station, Sun Valley, Idaho, USA

Topic(s): Willow
Category: Observational study (2) - Gray literature
Purpose: To explore the impact of native ungulates on YNP willow reproduction.
Conclusion: Elk over-browsing reduces seed production and colonization potential of willow. The number of seeds per m^2 of female willow canopy coverage inside ungulate exclosures ranged from about 109,000 for *S. geyeriana* to over 583,000 for *S. lutea*. Outside ungulate exclosures, no male or female catkins or willow seeds were produced.
Hypotheses: The following hypothesis was tested:
1) Intense browsing by ungulates limits willow sexual reproduction (SUPPORTED).
The following hypothesis / prediction was suggested:
2) Without abundant seed crops, willows cannot take advantage of recruitment opportunities produced by periodic large-scale disturbances such as fire.

Kay, C. E., and F.H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range: a critical evaluation of the "natural regulation" paradigm. Pages 151-169 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Willow, Aspen, Forest, Human, Fire
Category: Anecdotal (6) - Gray literature
Purpose: To compare early historic photographs and YNP's present-day.
Conclusion: Photos of aspen, willow, and coniferous forests taken from 1872 to the 1890's do not show evidence of ungulate browsing or highlining. Some early photos occasionally show conifers that lacked their lower branches, but this was likely caused by light ground fires or by human removal. Because historical photos of 100 year-old conifers and other woody vegetation show no evidence of ungulate use, few elk likely wintered in the park from the late 1700's through the 1870's. These photographs do

not support the Park Service's contention that Yellowstone was always a major elk wintering area and that the northern herd did not increase and alter the vegetation. Because these data do not support one of the key assumptions upon which natural regulation is based, that paradigm must be rejected.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) If the current number of elk in YNP is similar to the number prior to the park's establishment, historical photos should reveal that the condition of the park today is much like it was prior to it's formation.

Kay, C. E., and F. H. Wagner. 1996. Response of shrub-aspen to Yellowstone's 1988 wildfires: implications for "natural regulation" management. Pages 107-111 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Aspen, Fire, Climate, Human
Category: Observational study (2) - Gray literature
Purpose: To examine the factors that contribute to aspen growth and regeneration.
Conclusion: Only two-thirds of aspen clones depicted in early photographs survive today. Where shrub-aspen was found it only 20% of the area cover by the early aspen clones. Many stands that once contained thousands of aspen trees are now represented by small numbers of aspen. Burning did not stimulate shrub-aspen height growth, stem density, or clonal spread. Shrub-aspen at sites with additional soil moisture did not grow into trees even after they were burned, suggesting that climatic factors are unimportant. The only way for shrub-aspen to grow into tree-aspen communities will be to exclude ungulate browsing for 100 years.

Hypotheses: The following hypothesis was tested:
1) Shrub-aspen is a persistent community and all tree-type aspen will revert to shrub-aspen. (REJECTED)
2) Aspen will only grow into trees when stimulated by fire. (REJECTED)
3) Aspen will only grow into trees under ideal climatic conditions. (REJECTED)
The following hypotheses were suggested:
1) Ungulates are responsible for aspen community decline.
2) Long-term exclusion of ungulate browsing will be necessary for aspen to grow into trees.

Knight, D. H. 1996. The ecological implications of fire in greater Yellowstone: a summary. Pages 233-235 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Aspen, Willow
Category: Reference to another publication (7) - Gray literature
Purpose: To summarize the results of research on the 1988 Yellowstone fires.
Conclusion: Succession following the 1988 fires has been highly variable from one area to another. Aspen seedlings increased, but not in all burned areas. Browsing of aspen by elk continues to be heavy and has caused some aspen stands to persist only as shrubs. New willow sprouts became an important food in burned riparian areas. Burned forage, in combination with hunting pressure, low forage production during the dry summer, and a severe 1988-89 winter led to a 38-43% reduction in the northern Yellowstone elk herd. By 1993, the elk population had recovered.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Elk browsing will limit the reestablishment of new trees in burned Douglas-fir woodlands.

Knight, D. H., and L. L. Wallace. 1989. The Yellowstone fires: issues in landscape ecology. BioScience 39:700-706.

Topic(s): Fire, Aspen, Grassland, Forest
Category: Literature review (5) - Journal article
Purpose: To address fire-caused temporal and spatial variability in vegetation, plant animal relationships, and land-water interactions.
Conclusion: All landscape mosaics change over time, and it is unrealistic to expect that Yellowstone should not change as well. Fire will have a greater impact on big -sagebrush communities compared to other vegetation types because this species cannot root sprout. The loss of big sagebrush habitat may have had the greatest impact on mule deer and pronghorn, two ungulate species that rely heavily on big sagebrush as a winter forage. Approximately 25-30% of YNP was affected in 1988 by canopy fires, which greatly modified forest physiognomy. After fires, ungulates can establish new movement corridors linking water, bedding grounds, calving areas, and summer and winter ranges. Animals can influence rates of productivity and vegetation development, and thereby they could affect the development of the landscape mosaic.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Burned aspen will respond quickly to fire by root sprouting.
2) Vigorous growth of vegetation should occur in response to the 1988 Yellowstone fires.

3) Browsing by ungulates may increase post-fire due to increases in forage availability and possibly more nutritious sprouts.
4) Ungulate distributions responding to fire-caused changes in vegetation may have significant effects on nutrient transfer and productivity of different parts of the mosaic.

Knight, R.R., B.M. Blanchard, and P. Schullery. 1999. Yellowstone bears. Pages 51-76 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, eds. Carnivores in Ecosystems: the Yellowstone Experience. Yale University Press, New Haven, CT

Topic(s): Predator
Category: Literature review (5) - Book chapter
Purpose: To provide insight into YNP black bear and grizzly bear populations and their futures based on information gathered by past researchers. The paper's main focus is on the complexities involved in estimating population size and determining the ecological carrying capacity for YNP grizzly bears.
Conclusion: This paper largely focuses on YNP grizzly bears. Specifically, the authors discuss history related to effects of closing garbage dumps, population changes, and federal management. The only mention of elk is in a section on grizzly bear foraging strategies. Grizzly bears feed extensively on winter-killed and weakened elk and bison during March through May. Grizzlies are also efficient predators of newborn elk calves during May and June. Individual bears are known to be efficient predators of adult elk during the summer, although it is not thought to be widespread behavior in the population. Before 1968, documentation was lacking of substantial predation on elk, but recent observations have shown that this behavior has become more prevalent within the grizzly population.
Hypotheses: No hypotheses were tested or suggested

Lemke, T. O., J. A. Mack, and D. B. Houston. 1998. Winter range expansion by the Northern Yellowstone elk herd. Intermountain Journal of Sciences 4:1-9.

Topic(s): Human, Disease
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To examine and describe changes in northern Yellowstone elk winter distribution, population size, and harvests from 1975-1997.
Conclusion: Since the winters of the 1970's, northern Yellowstone elk have expanded their winter range by 41%. During this time, elk winter range north of the Park has more than doubled from 22,179 ha to 53,262 ha. Since 1988-89, the number of elk wintering north of the park has averaged 5460 elk/year. With more elk migrating outside the park, late season elk harvests increased 64% from 1979-1988 to 1988-1997. Winter range expansion, elk migration behavior, and increased winter harvests dispelled earlier concerns that winter hunts would prevent elk from using all available

winter range. Future challenges of managing Yellowstone elk north of the Park include: 1) harvesting enough elk to maintain the long-term diversity and productivity of winter range vegetation; 2) resolving land use conflicts with expanding elk into Paradise Valley; and 3) addressing growing concerns about the possible transmission of brucellosis from elk to domestic livestock

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Mild winters allow elk to use different areas and thus expand the winter range.

Margolin, J. H., and W. R. Jolley. 1979. *Sarcocystis* of elk (*Cervus canadensis*). Pages 226-228 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Disease

Category: Observational study (2) - Book chapter

Purpose: The effect of the parasite, *Sarcocystis,* on elk is unknown. This study attempted to gain basic information about *Sarcocystis* species in elk, to determine the suitability of the domestic dog as a definitive host for the *Scarcocytis* found in elk tissue, and to describe the development of sexual stages of the parasite in the dog.

Conclusions: The dog is a suitable definitive host for the species. Sexual stages were seen 5 to 13 days after inoculation. No signs of illness occurred during the prepatent or patent periods of the infection. Sporocysts were passed by all of the dogs begining 14 days after eating the infected elk meat and continued to be passed for 8 to 20 days.

Hypotheses: The following hypothesis was tested:

1) Coccidian sexual stages of the *Sarcocystis* species found in sheep and mule deer were found in the intestinal tracts of domestic dogs fed infected beef, so the dog will be a definitive host for the *Sarcocystis* found in elk tissue. (SUPPORTED)

The following hypotheses / predictions were suggested:

1) The high incidence of the parasite in Wyoming elk and the results of pathogenicity in other species suggests this species could be limiting the increase in herd and accounting for high calf mortality seen in herds.

2) A full range of native carnivores may serve as definitive hosts, which may play a role in the elk *Sarocycstis*.

Mattson, D.J. 1997. Use of ungulates by Yellowstone grizzly bears. Biological Conservation 81:161-177.

Topic(s): Predator, Human

Category: Experimental study (1) - Journal article

Purpose: To investigate the predator:prey relationship between ungulates and grizzly bears and evaluate how total ungulate use (or the frequency of predation by bears)

varies by ungulate species, availability of alternate foods, or annual and geographic variation in ungulate populations.

Conclusions: Elk comprised 53% of the ungulate meat consumed by grizzly bears in YNP. Thirty percent of this meat was procured by predation. Grizzly bears consumed scavenged adult male bison, scavenged elk <24 months-old, and killed and scavenged adult female elk. Predation on elk calves provided 4% of the total ungulate meat eaten by grizzly bears. Ungulates that died due to road kills, domestic livestock issues, and hunting bait accounted for 16% of total meat consumption by grizzly bears. Consumption of ungulates by grizzly bears was highest in spring and autumn and lowest in June and July. Predation contributed relatively little (9%) to the total meat consumed by grizzly bears during April and May, but contributed to 58% of total ungulate meat consumed in October. Elk calf predation was highest during calving season. Bears used adult female elk less than expected and elk calves more than expected. The frequency of ungulate use by grizzly bears was 2.1 times less during years when they used pine seeds. Predation by bears on elk was not positively related with elk group size.

Hypotheses: The following hypothesis was tested:
1) Variation in ungulate populations, alternate food availability, and geographic variation in ungulate numbers will affect grizzly bear behavior. (SUPPORTED)
The following hypothesis was suggested:
1) Grizzly bear predaton on ungulates varies inversely with whitebark pine seed production.

Meagher, M. 1989. Evaluation of boundary control for bison of Yellowstone National Park. Wildlife Society Bulletin 17:15-19.

Topic(s): Human

Category: Literature review (5) - Journal article

Purpose: To evaluate the effects of bison range control and its effect on the park ecosystem and public relations.

Conclusions: Fences and cattleguards were put up between Tower and Gardiner to block bison from migrating down the Yellowstone River Valley and out of the park. Location, fall and spring openings, and length of barriers were chosen to minimize the effects of elk migration. Visual inspection suggested that bison or elk broke some wooden slats, but both species detoured around the fenced areas. A fresh network of bison trails were observed heading toward Mammoth. Ungulates apparently moved at will. Fencing the entire northern boundary to halt bison migration out of the park would affect 17,000 elk.

Hypotheses: No hypotheses were tested or suggested.

Meagher, M., and M. E. Meyer. 1994. On the origin of brucellosis in bison of Yellowstone National Park: a review. Conservation Biology 8:645-653.

Topic(s): Disease

Category: Reference to another publication (7) - Journal article

Purpose: To summarize what is know about the origin of brucellosis in Yellowstone National Park.

Conclusions: Elk probably acquired brucellosis as a result of mingling with bison in the Buffalo Ranch wintering grounds. Elk in National Elk Refuge in Jackson Hole acquired the organism independently from cattle ranching on their wintering grounds. These elk summer in southern Yellowstone, but the likelihood of infecting bison or vice versa is slim.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Northern Yellowstone elk acquired brucellosis from bison.

Mech, D. L., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65:998-1003.

Topic(s): Predator, Topography [anecdotal (6)]

Category: Experimental study (1) - Journal article

Purpose: To answer questions about Yellowstone wolf predation on elk as it relates to winter severity.

Conclusions: Wolves tended to kill calves, old cows, and individuals with low marrow fat. More calves were killed in the milder winter of 1998 than the more severe winter of 1997. Cows killed were older than bulls. During one of the most severe winters on record, wolves had a higher killing success rate, killed more prey, and consumed less of each carcass than in the mild winter studied. The nutritional condition of the prey following the severe winter was poorer than the prey killed following the milder winter. A severe winter is not necessary for elk to become malnourished. The relationships between the reintroduced Yellowstone wolves and previously wolf-free elk did not differ from wolf-prey relations in long extant systems.

Hypotheses: The following hypothesis was tested:
1) Regardless of winter severity there will be enough elk in poor nutritional condition to support surplus killing by wolves. (SUPPORTED)
The following hypotheses / predictions were suggested:
1) The average age of wolf kills will be lower due to severe winter weather predisposing younger elk to predation.
2) There were more elk calves killed during the mild winter because more cows with calves migrate from wolf pack territories to lower elevations in severe winter weather.

Merrill, E., J. Hak, and N. Stanton. 1979. Responses of nematodes to ungulate herbivory on bluebunch wheatgrass and Idaho fescue in Yellowstone National Park. Pages 231-238 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Grassland

Category: Experimental study (1) - Gray literature
Purpose: To study the effects of above ground herbivory on below-ground nematode density and trophic structure.
Conclusions: Despite early seasonal differences in green biomass, by the end of the growing season green biomass of grazed plants of both *Festuca* and *Agropyron* equaled that of plants in the ungrazed areas. Above ground grazing by ungulates facilitates feeding by nematodes. Nitrogen concentration of green above-ground biomass was significantly higher in grazed plants. However, no difference was found in root nitrogen concentration in grazed and ungrazed plants
Hypotheses: The following hypotheses were tested:
1) Grazed plants should recoup their losses more rapidly so that there will be no detectable difference in above or below-ground biomass in a year of normal rainfall. (SUPPORTED)
2) Density of phytophagous and microbial feeding nematodes will not differ between grazed and ungrazed plants. (REJECTED)
3) Foliar nitrogen concentration is similar in grazed and ungrazed plants. (REJECTED)
4) Nitrogen concentrations of roots will differ in grazed versus ungrazed treatments. (REJECTED)
The following hypotheses / predictions were suggested:
1) Damage to root tips may stimulate lateral growth and support high densities of nematodes.
2) High densities of microbial-feeding nematodes found under grazed plants in May and June may be related to root mortality.
3) Increased microbial biomass and activity increases nitrogen mineralization.
4) Populations of phytophagous nematodes will not reach levels found under grazed plants because plants produce proportionally fewer numbers of root hairs, which serve as feeding sites for nematodes.

Merrill, E., and N. Stanton. 1990. Plant responses to spring grazing by elk in Yellowstone National Park (a preliminary report). Pages 147-150 *in* M.S. Boyce and G. Plumb, editors. 14th Annual Report: University of Wyoming, National Park Service Research Center. Laramie, WY, USA

Topic(s): Grassland
Category: Experimental study (1) - Gray literature
Purpose: To determine whether intense grazing of actively growing plants during spring plays an important role in the annual soil-plant-herbivore dynamic.
Conclusions: Standing dead biomass increases with time with significant differences between grazed and ungrazed plants by the end of the first season after rest from grazing. The amount of above ground green biomass in grazed areas was highest in September. In May and September, densities of plant parasites on both grass species were lowest under ungrazed species while bacterial feeders exhibited no obvious trends. Nematode abundance under Idaho fescue is more seasonally variable than under bluebunch wheatgrass. Analysis of data on root biomass is not yet complete, but the pattern of response appears different between species.

Preliminary results of changes in nematode composition and abundance indicate total densities were bimodal, with the highest densities under both species in May and September.

Hypotheses: The following hypotheses were tested:
1) Because senescing roots provide increased substrates for decomposers, microbial biomass and nitrogen mineralization should increase in response to grazing. (BIOMODAL; peaks in May and September)
2) Root biomass of grazed and ungrazed plants will be similar during spring grazing. (ANALYSIS INCOMPLETE)
The following hypotheses / predictions were suggested:
1) Under intense grazing in spring, grazed plants will initially show a decline in root biomass because photosynthesized assimilate will be allocated to regrowth.
2) Tiller density/unit of plant basal area will increase, and tiller length and weight will decrease as a result of spring grazing.
3) Nitrogen concentrations of soils, roots, and tillers will be higher in grazed than ungrazed plants in the spring.
5) Phytophagous nematodes will decrease under grazed conditions.
6) Dung (deposited during winter) as compared to litter-amended soils, will enhance mineralization processes.

Merrill, E. H., and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-273 *in* R. R. Keiter and M. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Grassland
Category: Experimental study (1) - Book chapter
Purpose: To examine the relation between summer forage dynamics on ungulate population dynamics.
Conclusions: Summer phytomass explained 77% of the variation in elk population growth rates after accounting for population size and weather effects. The proportion of cow elk with calves and the proportion of cow elk with yearlings at heel was significantly correlated with summer phytomass. Winter severity contributed significantly to variation in yearling recruitment, but not calf recruitment. If winter weather is milder and summer phytomass is higher, the carrying capacity will increase according to a quantitative relationship derived for the range.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Because survival and age of maturity are related to body weight, limited growth during summer due to poor nutrition may reduce recruitment and reproductive performance of elk.

Merrill, E., N. L. Stanton, and J. C. Hak. 1994. Responses of bluebunch wheatgrass, Idaho fescue and nematodes to ungulate grazing in Yellowstone National Park. Oikos 69:231-240.

Topic(s): Grassland

Category: Experimental study (1) - Journal article

Purpose: To measure the effects of nematodes on native grasses of the northern range especially in combination with aboveground grazers.

Conclusions: Grazing during the winter and early spring essentially removed all previous year's growth. Despite early-season differences, grazed plants recovered both belowground and above ground biomass by the end of the season. The number of flowering heads in ungrazed areas was higher than that of grazed. No grazing influence on tillering was found, although there was a decrease in the number of tillers in ungrazed areas due to small herbivores. Nitrogen concentration of above ground biomass was higher in grazed plants, but root nitrogen was not significantly different between grazed and ungrazed plants by the end of the growing season. Nematode densities showed a seasonal decline from May to July. Nematode densities did not significantly differ between treatments or grass species studied despite marked differences in root structure (many fine roots verses few coarse roots). Some groups of nematodes, including root-feeding, fungal-feeding and bacterial-feeding species, were significantly higher under grazed plants than ungrazed in May and June. This contradicts the hypothesis that phytophagous nematode density would be lower under grazed plants. The net effect of aboveground grazers is a redirection of carbon from decomposers to aboveground grazers and an increase in the rate of nitrogen cycling back to aboveground herbivores. This study implicates the importance of spring grazing and nematodes in these phenomena.

Hypotheses: The following hypotheses were tested:

1) Intense spring grazing increases root mortality. (SUPPORTED)

2) As a result of root mortality, root-feeding nematodes are higher because of the increased carbon availability for decomposers. (SUPPORTED)

3) As regrowth occurs, grazed plants recover above and below ground biomass because of low phytophagous nematode densities. (REJECTED)

4) Shoot and root N are higher because of high microbial activity and mineralization by bacterial-feeding nematodes. (SUPPORTED)

The following hypotheses / predictions were suggested:

1) Because of the close proximity of belowground herbivores to the decomposer food web, nutrient cycling in the plant-belowground herbivore system may be faster than the plant-aboveground herbivore system.

2) Microclimatic changes, resulting from indirect effects of grazing, may account for the difference in green biomass between grazed and ungrazed treatments.

3) Recovery of green biomass after spring grazing may be attributed to increased light saturation of the lower leaves, removal of transpiring tissue resulting in soil moisture conservation, or other belowground processes.

4) Defoliation arrests root growth and/or causes root mortality and is likely to contribute to lower root biomass of grazed plants in May.

5) Increases in phytophagous nematodes with grazing is due to an increase in root hairs.
6) Increases in phytophagous nematodes with grazing is due to a reduction in secondary chemicals that deter nematode feeding.

Murphy, K.M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. Ph.D. dissertation. University of Idaho, Moscow. 147pp.

Topic(s): Predator, Human
Category: Observational study (2) - Gray literature
Purpose: To investigate the interactions between mountain lions, their prey, bears, and humans in the northern Yellowstone ecosystem.
Conclusion: Cougar predation and reproductive success were studied from 1987 to 1996 in northern Yellowstone National Park and vicinity. Eighty-eight cougars were captured; 80 were radiocollared. Elk (Cervus elaphus) and mule deer (Odocoileus hemionus) comprised 98% of prey biomass and 81% of 302 cougar kills. Elk calves were the most important prey, mule deer were intermediate, and adult elk were least important relative to their availability. Cougars killed only 2-3% of elk and 3-5% of the mule deer on the study area each year. Cougar predation affected the size of the mule deer population more than elk because cougars selected elk calves preferentially to reproducing adults, but preyed upon the three sex-age classes of mule deer (fawns, does, and bucks) more equitably. The study's results supported Ackerman et al.'s (1986) conclusion that altering the sex-age structure of cougar populations (e.g., by hunting) could change the effects of cougars on the numbers and structure of their prey.
Hypotheses: No hypotheses were tested. However, the following hypothesis was suggested:
1) Altering the sex-age structure of cougar populations could change the effect cougars have on the numbers and structure of their prey.

Norland, J. E., and J. J. Reardon. 1996. Long-term sagebrush population dynamics and ungulate use at selected locations on the northern range of Yellowstone National Park. Yellowstone Center for Resources Natural Resources Report YCR-NR-96-4:1-30.

Topic(s): Grassland
Category: Observational study (2) - Gray literature
Purpose: To study the contrast of sagebrush communities in areas open and closed to ungulate browsing and compare the patterns of sagebrush demographics, evaluate sagebrush growth persistence, and understand the influence of patch and landscape dynamics.
Conclusions: Most sites are characterized by few long-lived sagebrush and many short-lived sagebrush which disappear in 25 years. Small-scale variation in soils is due to glacial material and landslide deposits that creates a patchwork of microsites each with a different potential for sagebrush growth. Sagebrush is an important forage

item for wintering ungulates because it is a good source of nitrogen and energy during a time when other forages are low in nitrogen and energy.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Belts with low sage brush coverage probably represent locations with poor soil for sagebrush, while belts with higher coverage are dominated by better soils.

Norland, J. E., F. J. Singer, and L. Mack. 1996. Effects of Yellowstone fires of 1988 on elk habitats. Pages 223-232 *in* J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Grassland, Willow, Forest

Category: Experimental study (1) - Gray literature

Purpose: To sample the short-term effects of the fires of 1988 on elk habitat use, elk forage biomass, elk forage quality, and snow characteristics in key elk winter habitats. To study the effects of the fires on willow biomass production, forage quality, willow morphology, and rates of use by elk to document whether or not fires enhanced willow status.

Conclusions: Elk habitat use patterns were unaltered within two years post-fire. There was no change in the diversity of grazed plants. There was no noticeable increase in shrub use by elk after the fires. Forage biomass did not increase in the burned areas, but decreased in areas where moderate soil heating was extensive. Forage quality measured by protein and digestibility increased on all burned areas during all seasons. Snow craters from elk grazing in winter were the same depth in burned and unburned areas, including burned Douglas-fir forests. Willow biomass increased, as did willow protein and digestibility concentrations. Ungulate herbivory increased on burned willows to such an extent that all burned willows were shorter three years post-fire than were unburned willows. Other factors such as the effect of the size and spatial arrangement of fires along with factors such as climate and population dynamics need to be further assessed.

Hypotheses: The following hypotheses were tested:
1) Elk will concentrate in burned areas due to increases in plant and landscape diversity and earlier and longer lasting periods of green forage. (REJECTED)
2) Elk diets will increase in diversity due to a change in palatability of burned forage, and grazing will shift to previously less palatable plants. (REJECTED)
3) Production of bunchgrass forages following some initial declines will increase dramatically over preburn levels, as will tissue nutrient concentrations. (REJECTED)
4) Burning will cause willows to have enhanced forage quality and higher production. (SUPPORTED)
5) Willow regrowth will have increased stature. (REJECTED)
The following hypotheses were suggested:
1) Changes in habitat use may occur more than two years after fires due to succession.

2) Willows in Yellowstone will not grow beyond the reach of fall browsers because they are water-stressed due to climatic change and lower water tables.
3) Elk in Yellowstone rarely use willow, but herbivory by even lower densities of elk are sufficient to keep burned willows short.

Pearson S. M., M G. Turner, L. L. Wallace, and W. H. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. Ecological Applications 5:744-755.

Topic(s): Fire, Grassland, Topography
Category: Observational study (2) - Journal article
Purpose: To examine the effect of fire and habitat heterogeneity on winter foraging of ungulates in northern YNP.
Conclusion: Burned areas were used more often than expected based on their availability, especially during mid to late winter, but the spatial pattern of burned areas (fragmented or clumped) was not related to grazing intensity. Ungulate grazing was greatest on low-elevation drier sites across the northern range and on steep south facing slopes. Grazing intensity was best predicted by environmental heterogeneity, especially the presence of burned areas, and topography (slope and aspect) at broader scales (e.g., >81,000 ha) rather than a per ha basis. This suggests that wintering ungulates in YNP respond strongly to coarse-grained variation in the landscape.
Hypotheses: The following hypotheses were tested:
1) Ungulate foraging behavior may be influenced by heterogeneity at the landscape scale. (SUPPORTED)
2) Ungulates preferentially use burned areas in the landscape for feeding. (SUPPORTED)
3) Ungulates preferentially use particular habitats or landscape positions for feeding. (SUPPORTED)
4) The geographic pattern of ungulate habitat changes through the winter. (SUPPORTED)
The following hypothesis / prediction was suggested:
1) Grazing in burned areas may result in enhanced forage procurement for ungulates in YNP.

Peek, J. M., A. L. Lovaas, and R. A. Rouse. 1967. Population changes within the Gallatin elk herd, 1932-1965. Journal of Wildlife Management 31:304-316.

Topic(s): Grassland
Category: Literature review (5) - Journal article
Purpose: To present data on population trends in the Gallatin elk population from 1932-65.
Conclusion: The general population trend of elk declined at about 2% per year during which time harvest intensity increased through the years and life expectancy declined. The general decline in population and age structures

of both sexes and the trend toward fewer males seemed largely the result of deteriorating amounts of winter forage, resulting from excessive grazing by elk over the previous 40 years.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Deteriorating winter forage supply should result in shifts in the age and sex structure of the Gallatin elk herd.

Reardon, J. J. 1996. Changes in grazed and protected plant communities in Yellowstone National Park. Effects of Grazing By Wild Ungulates in Yellowstone National Park. Pages 115-125 *in* F. J. Singer, editor. National Park Service Technical Report NPS/NRYELL/NRTR/96-01.

Topic(s): Grassland, Climate
Category: Observational study (2) - Gray literature
Purpose: To examine changes in species composition and shrub, forb and grass cover inside and outside exclosures over a 32 year period.
Conclusion: The exclosure of ungulates did not significantly affect vegetative cover. However plot and sample size limitation may have influenced the vegetative cover results. Species composition and rankings of dominant species fluctuated during the study period, but were not attributed do herbivore exclosure. The lack of stable or predictable species rankings may be indicative of the dominance of stochastic processes over other deterministic community regulation mechanisms.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Fluctuations in the species composition of the sites reflect the influence of abiotic factors such as short-term variation in weather.

Renkin, R., and D. Despain. 1996a. Notes in post-fire aspen seedling establishment. Pages 105-106 in J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Aspen, Forest, Fire
Category: Observational study (2) - Gray literature
Purpose: To examine post-fire establishment and growth of aspen seedlings.
Conclusion: Elk did not contribute to mortality of lodgepole pine or aspen, but competition between these species (at least for above-ground resources) has not yet been maximized. Even though 20-70% of the aspen seedlings experienced over-winter browsing each year, no differences in seedling height were detected inside and outside exclosures. Elk have not had a negative influence on aspen seedling height growth during the first 5 years post-germination at study sites located between 1800-2300 m.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Several factors contribute to aspen seedling survival and growth, including ungulate browsing and trampling, intraspecific competition, and competition with lodgepole pine seedlings.
2) At low elevations, elk browsing and trampling will likely keep aspen seedlings at reduced heights.
3) Aspen will likely succumb to competition with lodgepole pine in burned areas of the high elevation rhyolite plateau.

Renkin, R., and D. Despain. 1996b. Preburn root biomass/basal area influences on the response of aspen to fire and herbivory. Pages 95-103 in J. Greenlee, editor. Proceedings: second biennial conference on the greater Yellowstone ecosystem-the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Aspen, Fire

Category: Observational study (2) - Gray literature

Purpose: To determine if some aspen root properties could be quantified and correlated with standing crop variables, and if fire response may be determined by some pre-burn condition.

Conclusion: A curvilinear relationship between point estimates of pre-burn stem basal area and total root biomass was described. Both variables showed a significant positive correlation with the density, biomass, and average height of suckers produced during the first year following fire, as well as 5-7 years post-burn. Fenced exclosures and subplot isolation indicated that elk browsing influenced both sucker heights and age-class distribution, but had no effects on sucker density or mortality 5-7 years post-burn. Aspen are not necessarily predisposed to prolific growth following fire, but optimal response is observed in clones that occupy more suitable sites.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Shrub aspen is likely a consequence of the physical environment and reflects the inability of a particular site to support aspen as a canopy component.

Renkin R., D. Despain, and D. Clark. 1994. Aspen seedlings following the 1988 Yellowstone fires. Pages 335-337 in D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Aspen, Forest, Fire

Category: Experimental study (1) - Gray literature

Purpose: To (1) report ubiquitous aspen seedlings exclusively within burned areas of YNP, (2) describe morphological characters for distinguishing between recent seedlings and root suckers, and (3) use permanent transects and field exclosures for ungulates to describe early trends in aspen survival and growth.

Conclusion: Aspen seedling density was measured in 5 forested plots (4 unfenced, 1 fenced) and nine non-forested plots (7 unfenced, 2 fenced). Aspen seedling density ranged from 0.6 to 1014/m^2 in 1989. Average tallest heights ranged from 5.7 to 27.8 cm (mean = 12.8). On the 5 forested plots, the heights of lodgepole pine seedling ranged from 0.4 to 8.3/m^2 and from 1.9 to 3.6 cm (mean 3.0). Where aspen and lodgepole pine seedlings co-existed, aspen seedlings were 2 to 4 times taller than lodgepole pine seedlings. When plots were revisited in 1990, aspen seedlings were still found in all plots but densities were lower (range = 0.05 to 332/ m^2). Average tallest heights increased and ranged from 9 to 39 cm. Aspen inside exclosures were taller than aspen outside exclosures. The density of lodgepole pine was reduced in 2 plots, unchanged in 2 plots, and reduced to zero in another plot. Aspen seedling survival was influenced by the presence of ungulates, spring flooding, disease, and intraspecific competition. Assuming that the proportion of browsed, surviving seedlings reflected local ungulate density and utilization, ungulate presence negatively influenced seedling survival on the 11 unfenced plots. Ungulate presence did not influence lodgepole pine survival on 4 unfenced plots.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:

1) Ash generated from fires enhances soil moisture holding capacity and retention, thereby contributing to successful aspen establishment.
2) Hoof action of ungulates contributes relatively more to seedling mortality than browsing.

Ripple, W.J., E.J. Larson, R.A. Renkin, and D.W. Smith. 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227-234.

Topic(s): Aspen, Predator

Category: Observational study (2) - Journal article

Purpose: To compare aspen stands in high and low wolf-use areas to determine if there were significant differences in the number of elk pellet groups, aspen sucker heights, and the percentage of aspen suckers being browsed.

Conclusion: The aspen stands in high wolf-use areas had significantly lower counts of elk pellet groups in mesic upland steppe and the combined mesic upland steppe and riparian/wet meadow habitat types. Based on pellet group results, it appears that elk foraging behavior may have been altered by the increased risk of predation from reintroduced wolves. In the riparian/wet meadow habitat type, mean aspen sucker heights were significantly higher

in the high wolf-use areas than in low wolf-use areas. The percentage of browsed aspen suckers in high and low wolf-use areas was not different.

Hypotheses: The following hypothesis was tested:
1) Wolves may have an indirect effect on aspen regeneration by altering elk movements, foraging behavior, and browsing patterns. (PARTLY SUPPORTED)
The following hypotheses / predictions were suggested:
1) Ungulate anti-predator strategies may result in the avoidance of high wolf-use areas.
2) Because aspen is such a small component of the northern range landscape and is highly palatable to elk, even low population levels of elk could suppress aspen regeneration.

Romme, W. H., and D. H. Knight. 1982. Landscape diversity: the concept applied to Yellowstone Park. BioScience 32:664-670.

Topic(s): Grassland, Fire
Category: Predictive model (4) - Journal article
Purpose: To describe the natural changes that have occurred in landscape pattern over 240 years and the possible consequences of these changes for certain aspects of ecosystem structure and function and to examine forage, shelter, and water with respect to elk.
Conclusion: Within a given stand (5-ha), the quality of elk habitat has varied considerably over time due to changes in stand structure. However, at watershed level (73 km^2), there was much less difference in elk habitat quality over the 240 year period. Fire may not influence the overall quality of elk summer habitat on the high plateau of YNP. However, where meadows are less common, summer elk populations may fluctuate in response to changes in the upland landscape. Strong cyclic changes occur on areas of at least 100 km^2 in YNP, but more research is needed to determine if the landscape patterns in the park as a whole are in a state of equilibrium.
Hypotheses: No hypotheses were tested or suggested.

Romme, W. H., and M. G. Turner. 1991. Implications of global climate change for biogeographic patterns in the greater Yellowstone ecosystem. Conservation Biology 5:373-386.

Topic(s): Climate, Forest, Grassland, Topography
Category: Predictive model (4) - Journal article
Purpose: To explore the potential implications of global climate change for biogeographic patterns in the GYE by using conceptual models to compare likely climate scenarios.
Conclusion: Alterations in the distribution and extent of grassland communities resulting from climate change would affect the distribution and abundance

of ungulates. A warmer-drier climate would likely result in increased winter habitat inside the protected park. However, a warmer-drier climate could also result in reduced forage quantity and quality and offset the improvement of milder winter climate and an increase of winter range. If the climate were to become warmer and wetter, the treeline would likely move down in elevation and nonforest habitats at lower elevations would be reduced. A reduction in nonforest low elevation habitats could lead to smaller numbers of animals on winter ranges. However, ungulates may adapt and increase their use of forested habitats. Milder winter weather and increased forage production resulting from a warmer-wetter climate may also compensate for a reduction in the amount of nonforested habitat.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Alterations in the distribution and extent of grassland communities resulting from climate change will affect the distribution and abundance of ungulates.

Romme, W.H., M.G. Turner, L.L. Wallace, and J.S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone. Ecology 76:2097-2106.

Topic(s): Aspen, Fire, Predator [anecdotal (6)], Climate [anecdotal (6)]

Category: Observational study (2) - Journal article

Purpose: To (1) examine the spatial effects of the 1988 fires on browsing intensity of aspen by elk, and (2) conduct a historical analysis to uncover correlations and suggest additional mechanisms of the interactions between fire, elk, and aspen.

Conclusion: Density of sprouts in burned stands during 1990 (e.g., 2 years post-burn) was generally greater than in unburned stands. However, the density of sprouts in burned stands approached the density in unburned stands by autumn 1991. There were no differences in browsing intensity among burned, unburned-close, and unburned-remote stands in 1990 or 1991, nor were there differences among stands during these years in relation to growth from juvenile to adult sprouts. Unbrowsed sprouts were nearly all under the depth of the snowpack, suggesting that elk browse nearly all of accessible aspen sprouts. The conditions that existed in YNP during 1870-1890 when the current canopy stands of aspen were generated included: 1) relatively few ungulates; 2) the presence of large predators (wolves); 3) a wetter climate; and 4) recent, large-scale fires. A combination of all these factors is likely responsible for the paucity of aspen regeneration in YNP, rather than any single factor (i.e. elk browsing or fire suppression).

Hypotheses: The following hypotheses were tested:

1) The fires of 1988 stimulated such prolific sprouting of new aspen stems in burned stands that many stems will escape ungulate browsing and, therefore, regenerate a canopy of large aspen stems. (SUPPORTED)

2) Browsing pressure by ungulates is so intense that it inhibits aspen canopy regeneration in burned stands. (REJECTED)
The following hypothesis was suggested:
1) Changes in soil temperatures and the related production of auxins may account for the temporal pattern of sprout production after the 1988 fires.

Shovic, H. F. 1994. Landscapes of northwestern Yellowstone National Park: soils, landforms, and vegetation characteristics with interpretations of erosion potential and productivity. Pages 273-283 *in* D. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Topography, Climate
Category: Observational study w/o mechanistic explanation (3) - Gray literature
Purpose: To report on grass and shrub site productivity and erosion parameters for and their relation to landform, soil, and vegetation characteristics.
Conclusion: The ecosystems in the survey area result from landforms, soils and vegetation, all of which are influenced by a relatively dry climate. These factors (and past disturbances) significantly influence soil productivity, site productivity, and erosion potential. The intensity of these environmental variables may confound any apparent effects of present wildlife use.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Low soil productivity indicates that there are significant limitations to plant growth, such as high sodium or large numbers of rock fragments.

Singer, F.J. 1991. The ungulate prey base for wolves in Yellowstone National Park. Pages 323-348 in R.R. Keiter and M. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Predator, Fire
Category: Predictive model (4) - Book chapter
Purpose: To discuss the availability of ungulates to wolves inhabiting Yellowstone's northern winter range.
Conclusion: The northern range holds the greatest prospects for year-round wolf occupation because it is the winter range for the Greater Yellowstone Area's largest ungulate prey base. Elk population responses to the 1988 fires should take just a few years. The recovery of YNP's ungulates to population sizes equal to and, possibly, greater than pre-fire levels would likely occur before wolves are reintroduced into the Yellowstone.
Hypotheses: No hypotheses were tested or suggested.

Singer, F. J. 1996a. Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National Park. Pages 279-290 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. National Park Service Technical Report NPS/NRYELL/NRTR/96-01.

Topic(s): Willow, Human, Beaver [anecdotal (6)], Climate [observational study (2)]
Category: Experimental study (1) - Gray literature
Purpose: To examine the long-term trends in elk numbers, willow abundance, and browsing intensity on the northern winter range.
Conclusion: Two hypotheses for the decline in willows, the overabundant elk hypothesis and the warmer-drier climate hypothesis, are both well-supported. The author was unable to reject one in favor of the other. The secondary, defense chemistry hypothesis proposes that height suppressed willows will always be heavily browsed across a wide range of elk densities because of reduced defense chemistry and a reduced biomass potential under existing climate conditions.
Hypotheses: The following hypotheses were tested:
1) Elk are overabundant in the park because of the elimination of wolves, human disrupted elk migrations, and more elk wintering within the park than historically have in the past. (SUPPORTED)
2) A drier, warmer climate combined with a decline in beaver has resulted in reduced willow establishment, and willows are less able to sustain high levels of elk herbivory. (SUPPORTED)
The following hypothesis was suggested:
1) Reduced chemical defenses in height-suppressed willows, combined with a reduced biomass potential, both due to climate and water table reductions, act to keep willows in a heavily browsed and height-suppressed condition across a wide range of elk densities.

Singer, F. J. 1996b. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Pages 127-138 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. NPS/NRYELL/NRTR/96-01.

Topic(s): Grassland
Category: Experimental study (1) - Gray literature
Purpose: To evaluate the differences in above ground biomass production by plant species between grazed and ungrazed sites on Yellowstone's northern elk winter range.
Conclusion: No difference was observed in total standing crop biomass between grazed and ungrazed sites during the first year, but only about one-half the total standing crop biomass was produced on the grazed sites versus ungrazed sites the second year. The study was limited by the small number of replicate comparisons (n=10 paired macroplot comparisons) over only 2 years. The findings apply only to the upland bunch grass sites under study

and to sites where native ungulate herbivory was restricted to the winter period.

Hypotheses: The following hypotheses were tested:
1) Elk herbivory did not influence the frequency of grass, forb, or shrub species. (SUPPORTED)
2) Elk herbivory enhanced the protein content of live grasses. (SUPPORTED)
3) Bunchgrass mortality increases with elk herbivory. (REJECTED)
No additional hypotheses were suggested.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and the fires of 1988 on northern Yellowstone National Park grasslands. Ecological Applications 6:185-199.

Topic(s): Grassland, Fire
Category: Observational study (2) - Journal article
Purpose: To examine effects of elk herbivory and the 1988 fires on above-ground biomass production, N, and macronutrient concentrations, percent digestibility, and plant species composition in bunchgrass and big sagebrush communities, and the effect of the fires on elk habitat preferences.
Conclusion: Fire effects on elk forage were minor, however, elk preferred burned grasslands and gained some benefits perhaps due to greater foraging efficiency. Elk herbivory had a more important ecological effect on vegetation than fire. Grazed areas were higher in protein concentration, digestibility, macronutrients, and N. The lack of nutrient enhancement by the 1988 fires was attributed to elk herbivory, the relatively low accumulation of above-ground material, the high speed of the frontfire, and the resultant cool burning.
Hypotheses: The following hypotheses were tested:
1) Elk herbivory at 14-19 elk/km^2 results in a warmer, drier grassland with more bare ground, reduced plant biomass, and altered plant composition. (REJECTED)
2) Burning in grassland increases biomass, nutritional quality, and digestibility of forage consumed by elk. As a result, elk should prefer burned areas and exhibit an altered diet. (SUPPORTED; for grass and sage habitats)
3) The 1988 fall fires should increase quantity and quality of grassland forage less than prescribed spring fires. (SUPPORTED)
The following hypothesis was suggested:
1) The lack of nutrient enhancement by the 1988 fires was attributed to elk herbivory, the relatively low accumulation of above-ground material, the relative high speed of the frontfire, and the resultant cool burning.

Singer, F.J., and K.A. Schoenecker. 2003. Do ungulates accelerate or decelerate nitrogen cycling. Forest Ecology and Management 181:189-204.

Topic(s): Aspen, Grassland, Willow
Category: Experimental study (1) – Journal article
Purpose: To compare the ecosystem effects of ungulate herbivory on nitrogen cycling in two western national parks, Rocky Mountain (RMNP) and Yellowstone National Parks.
Conclusions: YNP grasslands fit the accelerating scenario for ungulate herbivory. In response to grazing at YNP, grassland plant species abundance was largely unaltered, net annual aboveground primary productivity was stimulated except during drought, consumption of key N-rich forages was moderate and their abundance was sustained, soil N mineralization rates doubled, N pools increased, aboveground N yields increased, and N concentrations increased in most grassland species. In contrast, grazing in grasslands in RMNP resulted in no detectable acceleration or deceleration of nutrient cycling. However, grazing effects in short willow and aspen vegetation types fit the decelerating nutrient cycling scenario. Willow and aspen types showed decreases in soil N mineralization rates, aboveground production, N pools, and aboveground N.
Hypothesis: The following hypothesis was tested:
Ungulate grazing in grassland, aspen, and willow communities may affect nutrient cycling (SUPPORTED)
The following hypotheses/predictions were suggested:
1) Higher rates of ungulate herbivory (~2X) in Rock Mountain N.P. could have contributed to the N deceleration there versus YNP.
2) The tendency of ungulates to move N between vegetation types on a daily basis in RMNP, but not in YNP, could have contributed to the observed N deceleration in RMNP.

Singer, F. J., and P. Schullery 1989. Yellowstone wildlife: population in process. Western Wildlands 15:18-22.

Topic(s): Fire
Category: Literature review (5) - Gray literature
Purpose: This article is a preliminary summary of findings by a variety of researchers and about some animals of special concern in the Yellowstone area.
Conclusion: A number of radio-collared elk altered their movements because of the 1988 Yellowstone fires. During the fires, elk were observed moving calmly and safely. After the fires a number of radio-collared elk traveled to the winter-range several weeks earlier than they had in 1987.
Hypotheses: No hypotheses were tested or suggested.

Singer, F.J., A. Harting, K.K. Symonds, and M.B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12-25.

Topic(s): Predator, Fire
Category: Observational study (2) - Journal article
Purpose: To understand factors influencing elk calf survival and mortality in YNP.
Conclusion: Calf survival in winter and summer was inversely related to elk population size in the previous winter. Most summer mortality was due to predation (22%), while most winter mortality was due to malnutrition. Summer survival was positively correlated with birth weight. Calf survival during the winters of 1987-1990 was positively correlated with early calving and mild winters, and inversely correlated with elk population size. Calf survival during the winter of 1988-89 was lower after drought and the previous summer's fires. Summer predation doubled after the drought and fires of 1988. Potential compensation in calf mortality was indicated by: 1) higher predation on light, late-born calves; 2) calves were lighter and born later after severe weather conditions; and 3) heavier-born calves survived at a higher rate. Summer mortality of calves due to predation was partly compensatory, but severe environmental conditions produced mostly additive mortality (e.g., increased summer predation, increased winter malnutrition). These results corroborate previous studies that suggest the density-dependent factors regulate the northern range elk population.
Hypotheses: The following hypotheses were tested:
1) Calf survival is inversely related to population density. (SUPPORTED)
2) Calf survival is related to body mass at birth and early birth date. (SUPPORTED)
3) Heavier, earlier-born calves survive at a higher rate. (SUPPORTED)
4) Calf survival is unrelated to environmental severity. (REJECTED)
5) Calf survival was reduced due to direct and indirect effects of the 1988 fires. (CONFOUNDED; neither supported nor rejected).
The following hypotheses / predictions were suggested:
1) Elk abundance will decline following wolf restoration.
2) Wolf predation will be compensatory with respect to elk calf mortality.
3) Wolf predation on elk neonates will be additive to other mortality.
4) Wolf predation will limit the elk population to 50-66% of current levels.

Singer, F. J., W. Schreier, J. Oppenheim, and E. O. Garton. 1989. Drought, fires, and large mammals. BioScience 39:716-722.

Topic(s): Fire, Climate, Grassland
Category: Predictive model (4) - Journal article
Purpose: To assess how drought on grasslands and fire influence elk abundance and distribution.

Conclusion: The study predicts an increased herbaceous and shrub layer, and a higher palatability of forages following the 1988 fires. Elk diets will likely be more diverse due to the projected increases in deciduous browse. Summer home ranges of elk and movements in burned and mosaic-burned areas are likely to be smaller than before burning, as a result of the increased plant productivity. The Yellowstone fires offer unique opportunities to address research questions. It is important to set up research programs immediately to follow long term aspects of the recovery process.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Depending on the severity of the winter conditions during the next few years, the size of the park's elk herds will likely increase as a result of the 1988 fires.

Singer, F.J., and J.A. Mack. 1999. Predicting the effects of wildfire and carnivore predation on ungulates. Pages 189-237 *in* Clark, T.W., A.P. Curlee, S.C. Minta, and P.M. Kareiva. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Grassland, Willow, Aspen, Fire, Climate, Predator

Category: Literature review (5) - Book chapter

Purpose: To review the history of ungulate management in the GYE and detail ungulate ecology prior to the fires of 1988 and the reintroduction of wolves. This book chapter also attempts to describe the short-term effects of fire and project longer-term effects on the habitat and populations of ungulates. In addition, the authors predict the effects of reintroduced wolves on predator-prey dynamics in this ecosystem.

Conclusion: Elk will remain the most-abundant ungulate in the GYE during the future because they will increase moderately as a result of the fires of 1988 and not decline substantially in abundance following wolf restoration.

Hypotheses: No hypotheses were tested or suggested.

Singer, F. J. and J. E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72:1383-1394.

Topic(s): Competition, Aspen, Grassland, Willow

Category: Observational study (2) - Journal article

Purpose: To report niche relations among elk, bison, mule deer, pronghorn, and bighorn sheep on the northern winter range of YNP.

Conclusion: During the time between the termination of elk-control and this study, ungulate numbers nearly tripled on the northern range. Elk and bighorn diets overlapped. Few other changes were observed between the 2 time periods. Four explanations are provided as to how total ungulate numbers could increase nearly 3 fold without evidence of any dramatic diet and habitat overlap among ungulate species.

Hypotheses: The following hypothesis was tested:
1) Increases in the numbers of elk and other ungulates will result in increased competition among ungulates. (PARTIALLY SUPPORTED)
The following hypothesis was suggested:
1) Increases in the use of sagebrush communities may reflect interspecific competition with elk.

Singer, F. J., and R. A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist 55:201-212.

Topic(s): Grassland, Topography
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To compare trends in big sagebrush abundance, structural characteristics, and annual production in browsed and unbrowsed sites.
Conclusion: Ungulate densities doubled at low elevations and tripled at high elevations during the study period. Shrubs constituted 8% of elk diets versus 81% of pronghorn diets. Ungulates restricted height, size, and recruitment of Wyoming big sagebrush at lower elevations, but not at higher elevations. Leader utilization was 8 times higher on low elevation winter range. Above ground biomass production did not differ between browsed and unbrowsed plots. Browsing appeared to suppress production, germination, and survival of Wyoming big sagebrush at low elevations. Numbers and cover of Wyoming big sagebrush declined 43% and 29%, respectively, from 1957-1990 on browsed areas along the Boundary Line Area. Big sagebrush leader use increases from 2% to 11% on higher portions of the winter range during the 1980s following cessation of elk controls.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435-443.

Topic(s): Willow, Beaver [anecdotal (6)], Climate [anecdotal (6)]
Category: Observational study (2) - Journal article
Purpose: To examine the effects of ungulate herbivory on willows on YNP winter range.
Conclusion: Many browsed-suppressed willows apparently grew on sites with lower growth potential than did tall or intermediate height willows, and thus were more vulnerable to the effects of large herbivore browsing. As predicted, height-suppressed willows possessed reduced concentrations of tannins, they were more highly preferred by ungulates, and off-take levels were higher than for taller willows. The authors conclude that xeric growth conditions during the last 100 years and a decline in the YNP beaver population may partly explain low willow growth, but that the proximate factor was herbivory by ungulates.
Hypotheses: The following hypotheses were tested:

1) Herbivory by large native ungulates is responsible for height suppression of willows on the northern range. (PARTLY SUPPORTED)
2) Drought-mediated water stress in willows results in reduced annual growth and contributes to height suppression of willows by large herbivores. (SUPPORTED)
3) Drought or herbivore-mediated reductions in potential defensive metabolites or increases in primary nutrients in willows increase palatability of willows to ungulates and subsequent suppression of willows. (SUPPORTED)
The following hypothesis was suggested:
1) Height suppression may allow willows to survive several decades of drought. Long-term existence in a suppressed-form will result in zero recruitment and subsequent disappearance of willow.

Singer, F. J., and R. G. Cates. 1995. Response to comment: ungulate herbivory on willows on Yellowstone's northern winter range. Journal of Range Management 48:563-565.

Topic(s): Willow, Climate
Category: Literature review (5) - Journal article
Purpose: To respond to a previous paper by Wagner et al. (1995) which criticized and refuted the results of a previous Singer et al. (1994) paper regarding willow decline in YNP.
Conclusion: The authors disagree with Wagner et al. (1995) that elk browsing is solely responsible for willow decline in YNP. Rather, they suggest that interactions among elk abundance, climate change, fire, wolf predation, and beaver abundance influence the status and recruitment of willow in YNP.
Hypotheses: No hypotheses were tested or suggested.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Topic(s): Grassland, Willow, Aspen, Fire, Climate, Human
Category: Literature review (5) - Journal article
Purpose: To evaluate the relative success or failure of the YNP natural-regulation philosophy in respect to management of ungulates.
Conclusion: Elk increased dramatically after 1968, but the evidence is equivocal for demonstrating the magnitude of any overabundance or overconcentration of elk. Evidence for the success of natural-regulation management of ungulates lies in the density dependence in the elk population.
Hypotheses: No hypotheses were tested or suggested.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors and persistence of willows in national parks. Wildlife Society Bulletin 26:419-428.

Topic(s): Willow, Beaver [anecdotal (6)], Climate
Category: Experimental study (1) - Journal article
Purpose: To compare trends in elk abundance, willow stature, elk consumption rates of willows, willow growth rates, climate trends, and beaver trends between Rocky Mountain NP and Yellowstone NP.
Conclusion: Growth conditions were better for willow in Rocky Mountain NP. Despite almost identical elk densities and rates of herbivory, willows in Rocky Mountain NP responded and compensated for elk herbivory and mechanical clipping better than willows in Yellowstone NP. Elk herbivory alone does not influence willow persistence or recruitment. In Yellowstone NP, a high density of elk contributed to the decline in willow heights, abundance, and seed production, but a negative elk influence on willow factors was not verified in Rocky Mountain NP, where growth conditions were better.
Hypotheses: The following hypothesis was tested:
1) Elk numbers are negatively correlated to annual heights and percent leader use of willows in Yellowstone. (SUPPORTED)
The following hypotheses / predictions were suggested:
1) If local water tables are reduced, water stress to willows could reduce rates of photosynthesis.
2) The beaver decline in Yellowstone may have exceeded a threshold value for willow persistence and recruitment.

Smith, D.W., L.D. Mech, M. Meagher, W.E. Clark, R. Jaffe, M.K. Phillips, and J.A. Mack. 2000. Wolf-bison interactions in Yellowstone National Park. Journal of Mammalogy 81:1128-1135.

Topic(s): Predator
Category: Observational study (2) - Journal article
Purpose: To describe interactions of introduced wolves and their large prey in YNP.
Conclusion: Wolves were more successful killing elk than bison because the elk were more abundant and easier to kill. Elk are the preferred prey of wolves in YNP when multiple prey species are available.
Hypotheses: The following hypotheses were tested:
1) Introduced wolves will take longer to kill 1 bison than 1 elk. (SUPPORTED)
2) Bison prey should be the most vulnerable individuals in a herd. (SUPPORTED)
The following hypothesis / prediction was suggested:
1) Bison will become regular prey for some wolf packs, at least during spring when bison are more vulnerable.

Stohlgren, T.J., L.D. Schell, and B.V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45-64.

Topic(s): Grassland, Climate [annotated (6)]
Category: Experimental study (1) - Journal article
Purpose: To examine grazed and ungrazed sites at multiple scales, determine the relative roles of grazing, soil, and climate in determining species richness, and generalize on the effects of grazing and cessation of grazing on plant diversity in Rocky Mountain grasslands.
Conclusion: At the landscape scale, grazing probably has little effect on native species richness and the accelerated spread of most exotic plant species. Grazing affects local plant species and life-form composition and cover, but spatial variation is considerable. Soil characteristics, climate, and disturbances may have a greater effect on plant diversity than do current levels of grazing. Few plant species show consistent, directional responses to grazing or cessation of grazing.
Hypotheses: The following hypotheses were tested:
1) Native species richness is lower in exclosures than in grazed sites. (REJECTED)
2) Grazed sites have higher native and exotic species richness than ungrazed sites. (REJECTED)
The following hypothesis / prediction was suggested:
1) Grazing alone cannot be implicated in directional changes in species cover and frequency in grazed versus ungrazed sites.

Taper M. L., and P. J. P. Gogan. 2002. The northern Yellowstone elk: Density dependence and climatic conditions. Journal of Wildlife Management 66:106-122.

Topic(s): Climate, Fire
Category: Observational study (2) - Journal article
Purpose: An examination of 1965-1995 aerial counts in understanding elk population dynamics using a variety of discrete time stochastic population models.
Conclusions: Density dependence in population growth rate is strongly supported. The herd is currently capable of regulating itself. The findings are in support of those by Turner et al. (1994d) and Wu et al. (1996) with respect to the suggestion that the 1988 fires were not responsible for the 1989-1990 herd decline. Further, the findings concur that elk habitat experienced a short-term (2-3 years) enhancement following the 1988 fires. The analysis should provide a strong background against which post-wolf introductions can be compared.
Hypotheses: The following hypothesis was tested:
1) Growth rate declines with population density. (SUPPORTED)
The following hypotheses / predictions were suggested:
1) The northern Yellowstone elk herd is self-regulating.

2) The fires of 1988 did not result in increased mortality but provided a temporary improvement in conditions. Herd decline during 1989-1990 was due primarily to the large 1988 herd size and drought conditions.

Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. Wildlife Society Bulletin 26:477-483.

Topic(s): Human, Disease
Category: Literature review (5) - Journal article
Purpose: To alert wildlife professionals to the potential pitfalls of habituated elk and the need for studies of the problem.
Conclusions: Elk habituation may result in management problems ranging from increased disease transmission to domestic animals and humans, to an over-riding evolutionary factor. Habituation may result from high-density elk populations and subsequent movement into human-dominated areas. Research is needed to develop strategies for describing and dealing with this potential problem.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Elk populations in the west will continue to grow and interact with humans.

Thorne, E.T., J.E. Morton, and W.C. Ray. 1979. Brucellosis, its effect, and impact on elk in western Wyoming. Pages 212-220 *in* M. Boyce and L. Hayden-Wing, editors. North American elk, ecology, behavior and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Disease
Category: Predictive model (4) - Book chapter
Purpose: To examine the impact of brucellosis on feed ranch elk in western Wyoming.
Conclusions: Infected elk can spread the disease to other elk and cattle through contact with aborted fetuses, newborn calves and associated birth tissues. Infection rate was about 50% in 2 herds. Eradication of the disease is recommended over control because of the continued high cost of the latter.
Hypotheses: No hypotheses were tested or suggested.

Tracy, B.F., and S.J. McNaughton. 1995. Elemental analysis of mineral lick soils from the Serengeti National Park, the Konza Prairie, and Yellowstone National Park. Ecography 18:91-94.

Topic(s): Grasslands, Geothermal, Competition [anecdotal (6)]
Category: Observational study (2) - Journal article
Purpose: To examine the pattern of mineral availability at licks in 3 globally significant grassland systems.

Conclusions: Na was the only mineral that was found in greater concentrations than soil at all 3 sites, and most forage is deficient in Na. This suggests that Na is an important reason that ungulates visit mineral licks. Importance of higher vitamin B and Ca concentration in hydrothermal licks at YNP warrants further study.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Hydrothermal licks may be important mineral sources for ruminants in YNP, and may reduce competition among animals.

Tracy, B.F., and S.J. McNaughton. 1996. Comparative ecosystem properties in summer and winter ungulate ranges following the 1988 fires in Yellowstone National Park. Pages 181-191 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the greater Yellowstone ecosystem – the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Grassland, Fire

Category: Observational study (2) - Gray literature

Purpose: To determine if fires influenced ungulate feeding patterns, and to measure impacts of fire and grazing on net aboveground production.

Conclusions: At the winter range site, net aboveground production, consumption by herbivores, graminoid N concentration, % soil moisture, initial extractable soil N and net P mineralization were higher in burned areas in the growing season 2 years after the burn when grazing was most intense. Ecosystem properties at the summer range site could not be correlated to fire or grazing activity.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) Production and consumption patterns in 1991 may have resulted from positive feedback involving intense fire and ungulate activity.

Turner, M.G., W.W. Hargrove, R.H. Gardner, and W.H. Romme. 1994a. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5:731-742.

Topic(s): Fire

Category: Observational study (2) - Journal article

Purpose: Examine the effect of fire size and distribution on the heterogeneity of YNP plant communities.

Conclusions: Most burned areas were within 200m of unburned areas, and thus, were nearby seed sources. Early season burns were less severe than those that occurred later in the season; the latter also burned over larger areas. These patterns may have an influence on plant recolonization/survival. The results of the analysis are complicated by the fact that the same fire may burn for several days and under varying environmental conditions.

Hypotheses: The following hypothesis was tested:
1) Heterogeneity of fires will increase with decreasing patch size. (PARTLY SUPPORTED)
The following hypothesis / prediction was suggested:
1) The establishment of opportunistic or invader species may be more likely in large patches, making the successional dynamics following very large fires more complex and less predictable than those of small fires.

Turner, M.G., W.H. Romme, and R.H. Gardner. 1994b. Landscape disturbance models and the long-term dynamics of natural areas. Natural Areas Journal 14:3-11.

Topic(s): Fire
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To develop insight into the periodicity, probability, severity, and extent of disturbances at the landscape scale at Yellowstone National Park.
Conclusions: Variability in the real Yellowstone landscape was greater than that simulated in the model. Landscape connectivity is an important factor that regulates disturbance dynamics. This information should be useful to managers in light of the increasing insularization of most preserves.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) The probability of a dramatic shift in landscape dynamics due to a rare disturbance event decreases with increasing reserve size.

Turner, M.G., W.H. Romme, and R.H. Gardner. 1994c. Relationships between spatial heterogeneity and large-scale fires on subapline plateaus in Yellowstone National Park. Pages 285-300 *in* D. Despain, editor. Plants and their environments: Proceedings of the first biennial science conference on the Greater Yellowstone Ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Fire, Forest
Category: Observational study (2) – Gray literature
Purpose: To examine the effects of disturbance history and post-fire patterns of burn severity on the reestablishment of lodgepole pine seedlings.
Conclusions: Mistletoe and pine beetle infestations in older stands increased the likelihood of crown fire. Early season fires were more responsive to spatial patterns of successional stages than those fires that occurred later in the burn season. High intensity fires appeared to kill the canopy seedbank. Basic floristic characteristics of burns remained similar to adjacent sites.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) The rate of plant reestablishment is influenced by the size of burned patch, the distance to the nearest unburned patch, and the amount and spatial distribution of burn severity.
2) Low seedling densities are likely due to severe fires that destroyed the canopy seedbank.

Turner, M.G., Y. Wu, L.L. Wallace, W.H. Romme, and A. Brenkert. 1994d. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications 4:472-496.

Topic(s): Fire
Category: Observational study w/o mechanistic explanation (3) - Journal article
Purpose: To explore the effects of fire scale and pattern on the winter foraging dynamics of elk and bison on the northern range using a spatially explicit individual-based simulation model.
Conclusions: Winter severity was an important determinant of ungulate survival. Fires that affected as much as 60% of the landscape did not reduce ungulate survival during the first winter post-burn. Fire is more of an issue during moderate to severe winters, however, the effects of these same fires may have beneficial impacts on ungulates in subsequent years. Winter survival was higher when fires were clumped versus small and patchy.
Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Resources are not limiting to ungulates when winter conditions are mild.
2) Fire size and spatial pattern of fire are important in severe winters.
3) A single large fire is not equivalent to a group of smaller fires with respect to ungulate survival.

Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411-433.

Topic(s): Grassland, Fire, Forest, Climate [anecdotal (6)]
Category: Experimental study (1) - Journal article
Purpose: To understand the effects of the 1988 YNP fires on plant succession and landscape/community heterogeneity.
Conclusions: An interaction of fire intensity, fire extent (patch size), pre-fire community, and geography affects the pattern of succession following fire. Climate change (a historical pattern of increasing aridity) may be an influence but was not measured.
Hypotheses: The following hypotheses were tested:
1) Biotic cover: decreases with increasing burn severity; is greater in smaller patches; exhibits no effect of distance to unburned forest. (PARTLY REJECTED)
2) Lodgepole seedlings: increase with increasing burn severity; density and cover are greater in smaller patches; decrease with increasing distance to unburned forest. (REJECTED)
3) Sprouts of forest herbs and shrubs: decrease with increasing burn severity; exhibit no patch size effect. (PARTLY SUPPORTED)

4) Opportunistic species: Increase with increasing burn severity; increase in larger patches; exhibit no effect of distance to unburned patches. (SUPPORTED)
5) Species richness: Increases in severe surface burns; decreases in light surface burns; lowest in crown fires; exhibits no influence of patch size; decreases with increasing distance to unburned forest. (SUPPORTED)
The following hypotheses / predictions were suggested:
1) Pathways of succession leading to nonforest communities were initiated following the 1988 fires.
2) Fire frequency in YNP may increase if future climatic conditions become warmer and drier.

Vales, D.J., and J.M. Peek. 1996. Responses of elk to the 1988 Yellowstone fires and drought. Pages 159-167 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the greater Yellowstone ecosystem – the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Climate
Category: Observational study (2) - Gray literature
Purpose: Examine effects of the 1988 fire on elk movements, mortality, diet, activity, and habitat selection.
Conclusions: Fire did not cause mortality in the sampled elk. Nor did it cause shifts in home range nor cause changes in migration timing. Fires on winter range affected the home range location of 12 of 20 study animals. Diets were more fibrous and had less forbs and grasses in the year immediately following the fire. Drought and fire in combination likely increased mortality during winter 1988-89.
Hypotheses: The following hypotheses were tested:
1) If not affected by fires, elk would remain within their summer home range and not use areas outside of it. (CONFOUNDED)
2) If affected by fire, elk would migrate to winter range no earlier than elk from ranges not affected by fire. (CONFOUNDED)

Van Dyke, F.G., J.P. Dibenedetto, and S.C. Thomas. 1991. Vegetation and elk response to prescribed burning in south-central Montana. Pages 163-179 *in* R.R. Keiter, and M. Boyce, editors. The Greater Yellowstone Ecosystem: Redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Fire
Category: Observational study (2) - Book chapter
Purpose: To quantify changes in elk forage quality and amount following fire, determine elk diets on winter range relative to burn history, and quantify elk use of burned areas.

Conclusions: Prescribed fire increases the nutritional quality of grasses and facilitates elk use for at least 5 years after burning. Recent fires in YNP should lead to increases in elk numbers. Controlled burns, repeated in 1-6 year intervals, in combination with unburned areas may provide improved nutritional conditions for elk by providing 2 distinct flushes of growth and a prolonged foraging period.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Elk use of burned areas may be a learned response.
2) Elk may be as attracted to quantity of vegetation as to quality.
3) Peak elk use may not coincide with peak plant nutrition.

Van Dyke, F.G., B.L. Probert, J.J. Rozema. 1994. Vegetation characteristics of elk summer range in south-central Montana. Pages 285-300 *in* D. Despain, editor. Plants and their environments: Proceedings of the first biennial science conference on the Greater Yellowstone Ecosystem. Technical Report NPS/NRYELL/NRTR. USDI, NPS, Denver.

Topic(s): Grassland

Category: Experimental study (1) - Gray literature

Purpose: To evaluate the importance of summer range forage quality in long-term productivity and persistence of elk populations.

Conclusions: Graminoids formed the bulk of elk diets, but diet varied among herds. Wet alpine sites provide a nutritional benefit especially during dry summers. Elk selected plants of higher nutrition in the more abundant plant categories.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) Elk populations that utilize higher quality summer forage exhibit higher productivity.
2) Moist sites may be important to elk during dry years by serving as reservoirs of high nutrition.

Van Dyke, F., M.J. Deboer, and G.M. Van Beek. 1996. Winter range plant production and elk use following prescribed burning. Pages 193-200 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the greater Yellowstone ecosystem – the ecological implications of fire in greater Yellowstone, September 19-21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Topic(s): Fire, Grassland

Category: Observational study (2) - Gray literature

Purpose: To examine the influences of fire on elk winter forage production, and recommend approaches for prescribed fire.

Conclusions: Graminoid and forb production increased and shrub production decreased from 1-5 years post-fire. Elk use peaked between 1 and 4 years post-fire.

Use was highest in areas where sagebrush was slow to reestablish. Longer (≥3 years) fire rotations may help elk establish use traditions and may facilitate the buildup of biomass for reburning.

Hypotheses: No hypotheses were tested. However, the following hypotheses / predictions were suggested:
1) An ideal burn schedule that optimizes graminoid protein levels may be impossible to achieve if there is insufficient biomass in heavily grazed areas to carry subsequent fires.
2) Longer burning rotations may optimize elk use in large herds because time is required to establish use traditions.
3) Longer rotations may reduce elk use and allow biomass buildup, shrub reestablishment, and permit reburning in heavily used sites.

Wagner, F.H., R.B. Keigley, and C.L.Wambolt. 1995. Comment: Ungulate herbivory of willows on Yellowstone's northern winter range: Response to Singer et al. (1994). Journal of Range Management 48:475-477.

Topic(s): Willow, Climate
Category: Predictive model (4) - Journal article
Purpose: Authors disagree with Singer et al. and their assessment that willow declines in YNP were the result of long-term changes in climate and hydrology.
Conclusions: Declines in willow are likely the result of a more complex suite of factors including heavier browsing that results from a non-random distribution of winter elk in lower elevations. They do not agree with the contention that chemical defenses of willow have declined during the 20th century. Not all tannins may be effective browse deterrents. Uses Kay (1990) photographic evidence to suggest that heavier browsing has occurred over the last century. The authors suggest that willow decline was caused by browsing from an overabundant elk herd.
Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) The progressive decline of woody vegetation on the northern range, especially willow, has been induced by a wintering elk herd that has greatly increased since establishment of YNP.

Wallace, L.L. 1996. Grazing and competition in montane grasslands. Yellowstone Center for Resources. Natural Resources Report YCR-NR-96-6.

Topic(s): Grassland
Category: Observational study (2) - Gray literature
Purpose: To determine grazing patterns of elk and bison in the northern range of YNP, and to determine if different grazing patterns influence the competitive interactions among major forage species.

Conclusions: Plants previously grazed were more likely to be regrazed, and there was a negative correlation between plant size and grazing intensity. Small, previously ungrazed plants are preferred by foraging ungulates.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:
1) The patchy distribution of nutrients deposited by grazing ungulates may account for the variability in compensatory response of the grazed plants as well as the variability in the amount of tissue removed.

Wallace, L.L., and S.A. Macko. 1993. Nutrient acquisition by clipped plants as a measure of competitive success: the effects of compensation. Functional Ecology 7:326-331.

Topic(s): Grassland

Category: Observational study (2) - Journal article

Purpose: To demonstrate grazing compensation via N uptake by clipped grasses.

Conclusions: A dominant grass in YNP exhibits compensation whereas a dominant grass from a tallgrass prairie does not. In both systems grazing promotes species diversity. Potential problems with study include lack of experimental controls and different soils in the 2 study areas.

Hypotheses: The following hypothesis was tested:
1) Clipped plants that exhibit compensation to grazing will exhibit the ability to procure N from the edge of a competitive radius. (SUPPORTED)
The following hypothesis was suggested:
1) In systems with a high proportion of compensating species, herbivory may enhance diversity because of increasing the competitive status of the grazed plants. In systems without many compensating species, herbivory will decrease the competitive status of grazed plants, thereby allowing ungrazed plants to become competitively superior.

Wallace, L.L., M.G. Turner, W.H. Romme, R.V. O'Neill, and Y. Wu. 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecology 10:75-83.

Topic(s): Grassland

Category: Observational study w/o mechanistic explanation (3) - Journal article

Purpose: To compare the spatial patterns of forage abundance in grazed and ungrazed portions of elk and bison range in the northern range of YNP.

Conclusions: At a fine scale feeding locations of large herbivores and rangeland biomass were distributed randomly. Forage biomass differed among communities (dry grassland, moist grassland, wet grassland, mesic grassland, understory), but forage quality did not. The authors suggest that ungulates feed randomly at fine scales but may be selective at broader scales.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) Ungulate feeding site selection may be based primarily on forage quantity at broad spatial scales.

Whitlock, C., S.C. Fritz, and D.R. Engstrom. 1991. A prehistoric perspective on the northern range. Pages 289-305 *in* R.B. Keiter, and M.S. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Topic(s): Aspen, Willow, Climate, Human
Category: Predictive model (4) - Book chapter
Purpose: To elucidate northern range conditions over a 14,000-year period using lake sediments and pollen data.
Conclusions: Aspen and willow have never been major components in the GYE (about 3%). Long-term trends over 14,000 years suggest great changes in plant community composition. However, over the last 150 years conditions on the northern range have remained within the spectrum of conditions exhibited over the last 200 years. The notion of increased erosion due to ungulate grazing was not supported. This synthesis supports the management philosophy of "natural regulation." Modern vegetation in the GYE developed over the last 1600 years. No direct or indirect influence of ungulate grazing was indicated in lake sediments.
Hypotheses: No hypotheses were tested or suggested.

Worley, D. E. 1979. Parasites and parasitic diseases of elk in the northern Rocky Mountain region: a review. Pages 206-211 *in* M. Boyce and L. Hayden-Wing, editors. North American elk, ecology, behavior and management. University of Wyoming, Laramie, Wyoming, USA.

Topic(s): Diseases
Category: Predictive model (4) - Book chapter
Purpose: A review of parasites and associated diseases in northern Rocky Mountain elk.
Conclusions: Elk are host to at least 23 endoparasites and 4 ectoparasites. Lungworms (*Dictyocaulus viviparous*) cause respiratory disease and are of greatest importance to the population. The other parasites rarely reach pathogenic levels.
Hypotheses: No hypotheses were tested or suggested.

Wright, R.G. 1998. A review of the relationship between visitors and ungulates in national parks. Wildlife Society Bulletin 26:471-476.

Topic(s): Human
Category: Predictive model (4) - Journal article
Purpose: Emphasizes the key role of public perception and education as a factor in management.

Conclusions: Parks must do a better job communicating complex management issues in order to regain an ability to manage.
Hypotheses: No hypotheses were tested or suggested.

Wu, Y., M.G. Turner, L.L. Wallace, and W.H. Romme. 1996. Elk survival following the 1988 Yellowstone fires: A simulation experiment. Natural Areas Journal 16:198-207.

Topic(s): Fire
Category: Observational study (2) - Journal article
Purpose: To model the interaction of the 1988 fires, elk herd size, and winter severity to evaluate the potential of implementing a prescribed fire program and in predicting effects of future fires on the northern range elk herd.
Conclusions: Calf mortality should be lower without fire, and overall elk mortality should be 7% higher with fire. Mild winters result in no fire-related mortality. Severe winters result in 100% calf mortality and 80-85% bull and cow mortality. Single patch or random fire distribution results in higher mortality. Higher initial elk density results in higher elk mortality, with a rapid rise in mortality when herd size exceeds 23,000. Overall mortality is likely exaggerated because the model restricts elk distribution to just the northern range within YNP.
Hypotheses: The following hypotheses were tested:
1) Mortality would have been lower without the 1988 fires. (SUPPORTED)
2) Mortality would be higher even with a less severe winter. (REJECTED)
3) Mortality would be different with different spatial burn pattern. (SUPPORTED)
4) Mortality would be lower with lower initial elk density. (SUPPORTED)
The following hypothesis / prediction was suggested:
1) A prescribed fire program that produces numerous, randomly dispersed, small burned patches will result in greater elk mortality if followed by a severe winter, than will a program that produces a single, large unburned patch of the same acreage.

Yochim, M.J. 2001. Aboriginal overkill overstated: Errors in Charles Kay's hypotheses. Human Nature 12:141-167

Topic(s): Human
Category: Literature review (5) - Journal article
Purpose: Examination of Kay's criticism of "natural regulation" in YNP, and claim that elk numbers are now much higher than in prehistoric times.
Conclusions: The author contends that Kay (1998) exaggerated claims of sources, failed to examine critical data, committed errors of omission, and used faulty logic. The evidence supports the notion that GYE ungulates were, in fact,

present in numbers comparable to those of today. Yochim suggests that the GYE offers an example of a pristine pre-Columbian landscape.

Hypotheses: No hypotheses were tested. However, the following hypothesis / prediction was suggested:

1) The issue may not be that Yellowstone has too many elk, but that other landscapes similar to it have too few.