Resilient Space: Bighorn Sheep (*Ovis canadensis*) Ecological Resilience in the Northern Rocky Mountains

by

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Abstract

Ecological resilience was defined, reviewed and discussed by synthesis of theory, concepts and empirical evidence presented in the primary literature (Chapter 1). Ecological resilience is concerned with ecological functions and the desirability of alternate states. Management and research are integrated with a focus on persistence of functions, stability of alternate states, responses to disturbance and regeneration, and accommodation of uncertainty and variability. Environmental quality strongly influences the tolerance to disturbance and therefore the resilience of a system or population.

The ecological resilience of bighorn sheep to 40 years of environmental variation, including a novel disturbance, was assessed from demographic patterns among census zones and over time (Chapter 2). Asymmetry in census zone productivity and population change determined distribution (immigration, emigration) in response to disturbance as the population process causing change. A reproductive potential of ewes as ~65% of adults, and a recruitment potential of lambs as ~20% of total bighorn sheep were demonstrated as measures of habitat quality that provide a safe operating space.

Environmental disturbance also changed the bioavailability of a hormetic (selenium), potentially increasing stress on ecological resilience (Chapter 3). Selenium levels from 85 ungulate populations from western North America were analyzed to identify a safe operating space of 0.06–0.30 ug/g. Selenium levels in populations outside of this interval always displayed low variability indicating individuals occupying low or high selenium environments were respectively always restricted in selenium uptake or unable to avoid high selenium uptake. Management for environmental quality to accommodate deficient or toxic selenium environments is discussed.

Management application of immediate technical actions and larger scale actions and a conceptual management framework with scenario examples are presented and discussed (Chapter4).

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Chapter 1

Ecological Resilience–A Review of the Concept and Application to Wildlife Conservation

Introduction

Managing for ecological resilience incorporates a well-substantiated set of theories and concepts. Early population management concepts to reduce variability and maximize yields, were advanced by the essential application of habitat management (e.g. Aldo Leopold, A Sand County Almanac 1949), and elevated to system level management of key processes and relationships of ecological systems (Allen et al. 2011). Resilience is concerned with the maintenance of functions and recognizes that some systems exist in more than one stable state (Holling 1973, 1986). However these capabilities have received limited application to wildlife management in Alberta and other North American jurisdictions. For instance how are ecological resilience concepts applied to studies of population dynamics and habitat quality?

We examine this question from the perspective of distribution, demographic attributes and response to human caused disturbance using bighorn sheep (*Ovis canadenis)* in the northern Rocky Mountains. This species and location is a good model to study ecological resilience because of the inherent ecological and social values of the species and the supporting ecosystem. The northern Rockies have expanses of limited anthropogenic disturbance and re-disturbance. Pre-Anthropocene (Holocene epoch) population and habitat function may persist and contribute to understanding adaptive capacity. However, high altitude environments are susceptible to climate change, and localized areas of highly modified landscapes are present. These opportunities to understand tolerance to disturbance facilitates development of effective management, including safe operating space (Rockstrom et.al 2009), to inform conservation and restoration management. Bighorn sheep winter abundance and composition data over the past 40 years are available to allow assessment of population change, demographic standards and distribution influence. Bighorn sheep may be particularly informative of environmental variation because habitat is contiguous in the northern Rocky Mountains in contrast to the fragmentation characteristic of more southern ranges. Horn growth consists of annuli which may inform of the significance of inter-annul variation in bioenergetics. Bighorn sheep genetics are relatively well understood, allowing assessment of population structure.

An established terminology has developed with the theories and concepts of resilience, which facilitates discussion and understanding, but does require explanation to achieve a common understanding among managers, researchers and publics. Additionally, to assess the influence of environmental variation, understanding the distribution and demographics associated with wildlife species presence, such as bighorn sheep, is required (Johnson 2007). Further, the increased complexity and differences in objectives and techniques to manage for ecological processes and safe operating space (see below) may not be adequately appreciated, relative to the proximal influence orientation of traditional population management (Allen et al. 2011). Application of resilience concepts may be limited because the nuances associated with terms used in the discussion of resiliency, and the importance of distribution and demographics to population vigour, are not appropriately appreciated. The goal of this introductory chapter is to provide familiarization with the concepts and terminology of resilience.

The Concept of Ecological Resilience

Resilience science is prefaced on the principles that ecological systems are continually in a transient state, and the persistence of relationships that perpetuate ecological systems is more important than the constancy of the system (Holling 1973). Resilience relies on examining major questions through the application of theory and practice (Curtin and Parker 2014), focusing on generic properties and processes and governance of systems (Biggs et al. 2012). The concept of resilience (introduced by Holling 1973) describes three aspects of ecological change over time (summarized by Gunderson and Allen 2010): (1) the “persistence of relationships within a system” determines the ability of a system to tolerate “changes of state variables, driving variables and parameters and still persist”, (2) systems may occur as alternate stable states as opposed to a single equilibrium state and (3) changes may occur in a surprising and discontinuous manner. These principles and aspects of resilience challenge the notion of stable equilibrium and therefore concepts such as carrying capacity and policies of sustained yield management (Gunderson and Allen 2010). Disturbance caused instability and variability advantages systems (Allen and Holling 2008) over a limited range beyond which excessive disturbance and variability can cause a shift to an alternate stable state (Holling 1996, Scheffer et al. 2001, Holling 2008). Excessive management-induced stability can reduce resilience and increase the likelihood of system collapse (Holling 1986, Holling 1996, Curtain and Parker 2014), or otherwise affect ecosystem values.

Resilience can be measured by the magnitude of disturbance and change that an ecosystem or population can tolerate without changing self-organizing processes and structures (Holling 1973, Holling 1986, Gunderson 2000, Carpenter et al. 2001). Benefits or liabilities associated with the persistent state are perpetuated (Walker and Salt 2012) because functions, feedbacks, structure and identity are retained while absorbing disturbance and undergoing change (Walker et al. 2004). Environmental quality (e.g. habitat quality) influences tolerance to the continual influences of disturbance and regeneration and therefore affects resilience and the properties of self-organization (Holling 1973, Holling 1986, Carpenter et al. 2001, Walker and Salt 2012).

Self-organization refers to interactions among internal ecological factors (e.g. components) and scales that control ecosystem functions. Self-organizing systems are characterized by emergent properties, which may not be predictable by component parts of ecosystems, and may have persistent effects on ecosystem quality or population vigour (Holling 1986, Walker and Salt 2012). Surprising responses to change in ecological systems should be expected because of emergent properties and insufficient knowledge of how particular ecosystems function (Holling 1973, Doak et al. 2008, Lindenmayer et al. 2010, Curtin and Parker 2014). Management and information collection initiatives that rely on “excessive” reductionism can impede effective conservation of ecosystems and populations (Holling 1973, Doak et al. 2008, Curtin and Parker 2014), including integration with potential or realized human-caused disturbances.

The ability to self-organize without changing process and structure is greater where disturbance agents are internal co-evolved ecosystem components rather than external drivers (Carpenter et al. 2001). Co-evolved ecosystem components are exemplified by: (i) symbiotic relationships between herbivores and vegetation; (ii) the processes of aging, decomposition and regeneration of forest stands; and (iii) internal population regulation by predators in response to prey availability. External drivers resulting in novel disturbances (e.g. human-caused disturbances from resource extraction or climate change) or extreme natural disturbances (e.g. hurricanes, prolonged severe drought) may exceed the capacity of internal interactions to sustain the pre-disturbance system and sustain ecological benefits.

Ecosystem benefits (goods and services) such as wildlife species, plant productivity or water quality and quantity are among the ecological values of primary interest to societies. Wildlife conservation is primarily interested in the persistence of the states of ecological communities and constituent populations and the value of habitat (locations occupied) to population vigour (Van Horn 1983, Krausmann 1999, Pulliam 1988, Garshelis 2000, Schlaepfer et al. 2002, Mills 2007, Galliard et al. 2010, Holt 2011, Pulliam et al. 2011).

Attributes of wildlife populations (e.g. abundance, age and sex composition, productivity and distribution) and plant communities (e.g. annual productivity) termed *“fast variables”* are shaped by interactions with ecosystem variables that change more slowly (e.g. soil composition, vegetation community structure, phenology, precipitation and melt/runoff rates, nutrient availability, scalar relationships), which are termed *"slow variables"* (Walker et al. 2012). *Fast* and *slow* refers to relative rates of change, not absolute rates (Walker et al. 2012). The structure of social-ecological systems is determined by the slow ecological variables, which are often linked to regulation of ecological conditions (Biggs et al. 2012). Interactions and feedbacks among fast variables responding to conditions created by slow variables typically determine the dynamics of a system (Holling 1986, Biggs et al. 2012, Walker et al. 2012). *External drivers* (e.g. societal demands to extract resources, climate, weather) or other controlling variables interact with and modify slow variables, potentially altering the state of wildlife populations (Holling 1986, Walker et al. 2012). Slow variables shape how a fast variable will respond to changes in an external driver (Walker et al. 2012).

Population state is a function of abundance, composition, and distribution phenomena at spatial scales defined by demographic or genetic populations (Hampton et al. 2004, Esler et al. 2006, Palsboll et al. 2006, Johnson 2007, Mills 2007, Estes-Zumpf et al. 2010; Lowe and Allendorf 2010). Considerable ability to quantify the presence and locations selected (habitat use) by wildlife populations is available from direct observation (e.g. systematic surveys) and techniques associated with Geographic Positioning System and camera technology. However, determining the value of locations to population persistence (habitat quality) is more complex, requiring understandings of demography and distribution (Johnson 2007), and is fundamental to determining population state.

Habitat quality informs demographic measures that depend on the contribution of the occupied area to the probability of population persistence (Van Horne 1983, Pulliam 1988, Krausman 1999, Thomas and Kunin 1999, Garshelis 2000, Perkins et al. 2003, Bock and Jones 2004, Nielsen et al. 2006, Johnson 2007, Mills 2007, Johnson and Seip 2008, Gaillard et al. 2010). Demographics incorporate variation in vital rates and distributions that occur in response to environmental variation at spatial or temporal scales (Holling 1986, Boyce et al. 2006, Mills 2007). Habitat quality reflects environmental quality and is not necessarily predicted by habitat selection. An inverse relationship between habitat quality and selection can exist, particularly at locations where the environmental conditions result from human disturbance (Pulliam 1988, Donovan and Thompson 2001, Schlaepfer et al. 2002, Delibes et al. 2001, Battin 2004, Hobbs et al. 2009, Sih et al. 2011, Sih 2013).

Human activity has altered the nature of ecological change, including: increasing rates of change, increasing or suppressing variability associated with evolutionary influences and introducing ecological elements that have not co-evolved with native wildlife species (e.g. Holling 1973, Holling 1986, Scheffer and Carpenter 2001, Carpenter et al. 2001, Boyce et al. 2006, Hobbs et al. 2009, Sih et al. 2011, Sih 2013). Responses to novel disturbance, including reorganization, are potentially significantly different from those resulting from evolutionary relationships (Hobbs et al. 2009, Sih et al. 2011, Sih 2013). Human influence on ecological systems has increased (1) uncertainty associated with the determinations of status and apparent habitat quality, (2) the urgency to develop assessment methodologies and contingencies (3) and the imperative to associate ecological processes with sociological (includes economic) and governance influences (Biggs et al. 2012, Walker and Salt 2012, Curtin and Parker 2014).

Resilience science is a discipline providing concepts, perspectives and methodologies to assess ecosystem response to, and societal governance of, natural and human disturbances (Walker and Salt 2012, Biggs et al. 2012, Curtin and Parker 2014). Some constituents of ecological resilience can be quantified, but the point is assessment of the system. Assessment is concerned with the quality of the system (Holling 1986) favouring broad relevant scientific questions and accuracy (Curtin and Parker 2014).

Resilience Versus Stability

Holling (1973) distinguished between resilience and stability (Fig. 1.1) to facilitate discussion and avoid confusion. Resilience is the system property that results in persistence or probability of extinction (Holling 1996). Stability is the system property that results in the degree of fluctuation around equilibrium; measured by the speed of return to, and fluctuation from equilibrium, when subjected to a temporary disturbance (Holling 1996).

Two fundamentally different definitions of resilience are generated by contrasting aspects of stability (Holling 1996). *Engineered resilience* is concerned with maintaining the *efficiency of function (*Fig. 1.2*)*; attempting to minimize fluctuation and emphasize equilibrium by a focus on efficiency, constancy and predictability (Holling 1973, Holling 1996). Efficiency of function is exemplified by targeting the maintenance of a specific population size or harvest rate, under the assumption that the resources supporting the population and benefits generated by the population are being most efficiently used.

Ecological resilience is concerned with maintaining the *existence of function (*Fig. 1.2*)*; focusing on persistence, adaptation to change, variability, and unpredictability, including the constructive role of instability (Holling 1996). Ecosystems with resilience properties can vary substantially from equilibrium at points in time and space (Fig. 1.2) (Holling 1973). High quality environments characterized by complexity, diversity, and redundancies (Holling 1986), co-evolved ecosystem components (Carpenter et al. 2001), and feedbacks with internal system components (*slow variables*) that structure the system (Biggs et al. 2012) are believed to allow for maintaining ecosystem function (Fig. 1.2). The persistence of function provided by these processes and properties may be lost by attempts to maintain the efficiency of function through human activities such as sustained yield management. The objective of ecological resilience is to maintain variation in a population within a desired state (Fig. 1.1) over an extended time. Existence of function is exemplified by maintaining soil building capabilities; the capability of plants to vary growth in response to changes in weather and exploitation by herbivores; synergistic relationships between vegetation and herbivores; and capability of wildlife populations to vary vital rates or distribution in response to bioenergetics of temporal resource availability and use.

Resilience emphasizes adaptive management (Holling 1973; Holling 1996). If environmental quality can absorb and accommodate future events the ability to predict the future is not needed. The variable that reduces the resiliency is what is important while the proximate cause of change may be unimportant. For example the reason why unsustainable harvest or predation occurred (e.g. increased vulnerability, landscape change, apparent competition, and demand for resource extraction) is the issue, not the actual harvest or predation rate; the reason why the death of one adult female grizzly bear(*Ursus arctos)* is a conservation concern is important, not the actual death of a female grizzly bear.

Alternate Stability Regimes

Resilience recognizes that more than one stability state (regime or domain) may occur, so that ecosystems can shift between multiple stable states (alternate domains of attraction)(Fig. 1.1) (Holling 1986, Holling 1996, Peterson 2008, Curtin and Parker 2014). Each state exhibits a difference in structure, function, and qualitative nature (Fig. 1.2) (Holling 1986, Peterson 2008). State shifts are changes that are persistent, relatively large and typically abrupt (Fig. 1.2) (Holling 1986, Scheffer et al. 2001, Folk et al. 2004). Multiple stable states (shifts between regimes or domains) were proposed based on changes first documented in boreal forest ecosystems (Holling 1973, Holling 1986).

A review of the evidence of regime shift documented 45 multiple state regimes in 15 major ecosystems characteristic of freshwater, marine, forest, savannah and grassland and Arctic/sub-Arctic ecosystem types (Folk et al. 2004). These authors suggest that a focus by some researchers on measuring stability may have resulted in missing the presence of state shifts. Detecting and managing for state shifts requires purposeful effort (Scheffer and Carpenter 2003, Folk et al. 2004), because of the involvement of heterogeneous systems, more than one spatial scale and multiple causes that may play out over many years (Carpenter and Brock 2003).

Regime shifts involve changes in feedbacks controlling key processes at different space and time scales (Fig. 1.3) (Holling 1973, Carpenter and Brock 2006). Ecosystem components may change in a discontinuous manner when attraction to a different equilibrium condition causes transition to another state (Holling 1986). State shifts have prolonged consequences because they result from substantial reorganization of complex systems (Brock et al. 2008) and produce emergent properties that may be unpredictable. Resilience is therefore concerned with: (i) how much disturbance a system can absorb; (ii) the degree to which the system can self-organize; (iii) the degree that learning and adaptability can occur (Carpenter et al. 2001). Within a state it is the fact of equilibrium that is the important consideration, not the precision of variation (Holling 1986).

Ecological resilience is concerned with events distant from equilibrium near the boundary of a stability regime (Holling 1996). Shifts between states can happen rapidly, changing the fundamental nature of the system (Holling 1973, Scheffer et al. 2001, Folk et al. 2004, Levin 2008). Stress on an ecosystem or population with a state positioned near the threshold (Fig. 1.2) typically yields larger, more rapid changes, and probability of a state change, than stress on a state well within the internal bounds of a deep domain (Scheffer et al. 2001). Large domains are less prone to shifting to an alternate state. The size of the stable state domain, or the amount of disturbance required to shift the state, can be increased or decreased by influencing environmental quality (e.g. habitat quality). Environmental quality provides populations with a tolerance to variations in slow variables and disturbances by external drivers (Holling 1986, Walker and Salt 2012). Addressing the gradual changes that affect resilience is expected to be the most productive approach to sustaining a desired state or promoting change from an undesired state (Scheffer et al. 2001, Biggs et al.2012). Large magnitude changes typically result from an accumulation of smaller internal changes, sometimes with combined or synergistic effects, that make ecosystems and populations vulnerable to transitions that may be catastrophic and occur without warning (Scheffer et al. 2001, Folk et al. 2004).

Persistence of Relationships - Ecosystem Functions (Adaptive Cycle), Complexity and Feedbacks

The adaptive cycle (Fig. 1.4) expanded the concept of ecological succession to distinguish the four ecosystem functions of exploitation, conservation, release, and reorganization (Holling 1986, Curtain and Parker 2014). Holling recognized that the exploitative (binding of nutrients, accumulation of biomass, modification of the environment) and subsequent conservation (highly organized trophic and competitive connections) phases did not capture the periods of disorganization that are inherent in systems of discontinuous change. Holling therefore proposed that phases of release (system breakdown) and reorganization (restructuring, development of connections) are essential considerations in understanding resilience and change in ecosystems. Reorganization is the most probable phase for a shift to an alternate stability regime to occur (Holling 1986, Carpenter et al. 2001, Walker and Salt 2012, Curtain and Parker 2014).

The adaptive cycle depicts self-organizing systems, which are also termed as complex adaptive systems. Complexity is characterized by: components that are independent and interacting (Fig. 1.3); components and interactions that are affected by selection processes; and the constant addition of variation and novelty (Walker and Salt 2012), and is critical to understanding resilience (Curtin and Parker 2014). Critical ecosystem parts can function independent of each other. Reponses to changes or threats may be limited in under-connected systems, exemplified by fragmented landscapes exposing wildlife populations to disturbances causing risk (e.g. human intolerance, predation, high cost food resources). Over-connected systems can become brittle, unable to respond to stress and prone to collapse (Holling 1986, Walker and Salt 2012, Curtin and Parker 2014). An over-connected system is exemplified by a large forested area of even aged and common composition stands, which are vulnerable to spread of disturbances such as fire or insects.

Complex systems involve a hierarchy of scales (Fig. 1.3). Landscapes form a hierarchy with breaks at particular scales (Holling 1992). Holling (1986) proposed that a scale was a community where interactions between organisms determine system behaviour more than do external events. Scales become parts of larger scales through external links (Holling 1986) that are commonly expected to strengthen resilience. In some instances resilience can be achieved at specific time or spatial scales because of subsidy from broader scales, resulting in a disparity that may jeopardize the persistence of the systems (Carpenter et al. 2001). Connectedness can facilitate both the (1) extent of the disturbance consequences and (2) recovery from disturbance (Nystrom and Folk 2001, Biggs et al. 2012).

Feedbacks form the relationships between organisms within a scale and among scales, and are essential in determining states achieved in complex systems (Fig. 1.2). Feedbacks between “fast” and “slow” variables determine the equilibrium levels and the variation within a stable state (Holling et al. 1986, Holling 1992, Walker et al. 2012). Slow variables create the conditions that determine the structure and nature of a system, while interactions and feedbacks with and among fast variables generate the dynamics of the system (Biggs et al. 2012). Typically only a small number of slow variables control a system at any scale (Holling et al. 1986, Walker and Salt 2012). Positive feedbacks reinforce a particular relationship, while negative feedbacks counter particular relationships. Equilibriums that locate at the edge of basins of attraction increase the risk of regime shift, warranting precautionary approaches (Doak et al. 2008).

Notably there are no feedbacks from a complex system to external drivers (Fig. 1.2) (Walker et al. 2012). Fast variables will respond to external drivers, but feedbacks will not develop. For example, where an external driver of human origin (e.g. harvest or habitat alteration) removes individuals of a population, the interaction among the remaining population members, and with other fast variables (e.g. populations of other wildlife species, forage opportunities), within the structure established by the slow variables (e.g. vegetation community structure, spatial association of ecological units) will significantly affect tolerance to the external driver. If response is adverse, modification of the external driver may be required if persistence of the population is desired. Environmental quality will determine the ability to tolerate the stress from the external driver.

Surprises

Ecological surprises offer important benefits because they teach us how to best interact with the environment (Doak et al. 2008, Lindenmayer et al. 2010). Ecological surprises (1) challenge and revise understandings of environmental structure and process; (2) allow assessment of existing assumptions; (3) trigger subsequent studies that lead to significant discoveries, and (4) facilitate questioning of resource management effectiveness (Lindenmayer et al. 2010). Surprises occur when the responses of natural systems are greatly different from human expectations of the causes of observed events, the behaviour of system elements, and the responses to actions (Holling 1986). Surprises are findings outside the envelope of outcomes expected to occur or not occur (Lindenmeyer et al. 2010) and that stretch human knowledge.

Emergent properties associated with self-organizing systems make surprise likely, common (Holling 1986, Lindenmayer et al. 2010) and inherent to all ecological systems (Doak et al. 2008). The frequency of surprises in ecological systems is expected to increase due to changes in interacting environmental stressors such as climate change and land use (Lindenmayer et al. 2010) and increasing environmental variability (Boyce et al. 2006). Detecting and analyzing surprises or unexpected findings are critically important to advancing ecological understanding and natural resource management (Doak et al. 2008, Lindenmayer et al. 2010).

The importance of surprise and uncertainty obliges development of anticipatory capacity (Lindenmayer et al. 2010). Highly precautionary and adaptive management, rather than approaching and testing thresholds, are required to accommodate surprises (Doak et al. 2008). Timely detection of changes in the environment is essential to effective management (Contamin and Ellison 2009). Environmental extremes resulting from complex and coincidental interactions of common factors can influence ecological dynamics as much as average effects (Denny et al. 2009), rendering the nature and magnitude of environmental modifications unpredictable. Precautionary and adaptive management contingencies are required in addition to rigorous scientific question development, information collection, and analysis (Doak et al. 2008). Detecting and analyzing surprises or unexpected findings are critically important to advancing ecological understanding and natural resource management (Lindenmayer et al. 2010).

Discontinuities

Discontinuities, breaks in continuous distribution and departures from scaling laws (Holling 1992) have been documented in ecological, biological, and anthropogenic systems (Allen and Holling 2008). Attributes (e.g. body mass clumps, vegetation structure) of complex ecosystems are distributed discontinuously (Holling 1986, Holling 1992, Holling et al. 2008). Dominant processes and structures within a scale range produce discontinuities in spatial and temporal frequencies (Fig. 1.3) (Holing 1986, Gunderson and Holling 2002, Holling et al. 2008). These mutually reinforcing sets of processes operating in a hierarchy of different spatial and temporal scales, separated by discontinuities in key variables, are termed panarchies (Fig. 1.3)(Gunderson and Holling 2002).

Ecological panarchy might create discontinuities for two reasons (Holling et al. 2008). First, processes forming the panarchy are discontinuous resulting in separation of scales for key structuring variables (e.g. see Holling 1986 spruce-budworm (*Choristoneura occidentalis*) boreal forest; one year budworm and spruce (*Picea sp.*) needles; 12–15 year generation – tree crown; 100–year plus tree stand (Fig. 3)). Second, the four phases of the adaptive cycle are distinct (Fig. 1.4). Shifts from one phase to another are abrupt because the shift is nonlinear. Each phase creates distinct conditions.

Large, unexpected changes in ecosystem services may also result from incremental stresses causing regime shifts (Brock et al. 2008). These types of discontinuous change occur because there are multiple stable states (Holling 1986). An approaching threshold, or impending state change, may in some instances be predicted by discontinuities or changes in variance or correlations (Carpenter and Brock 2006, Scheffer et al. 2009, Scheffer et al. 2012, Lentonin 2013). Rapid change occurs after periods of gradual change when different equilibria suddenly occur and other equilibria disappear (Holling 1986).

Thresholds

Thresholds bound a safe operating space, allowing understanding of the system, and limits to the influence societies may have if the system is to persist (Rockstrom et al. 2009). In ecology, thresholds are used to analyze changes in state, the influence of external factors, and critical loads that can be assimilated (Scheffer and Carpenter 2003, Groffman et al. 2006). Thresholds are discontinuities that provide warning of an impending state change because feedbacks have changed; the system will change trajectory or rates and the state may change abruptly (Fig. 1.2) (Holling 1986, Holling 1996, Folk et al. 2004, Peterson 2008, Walker and Salt 2012, Curtin and Parker 2014).

Consideration of thresholds may vary with a scale of interest that has ecological or social integrity. Systems may be characterized as no threshold, a stepped threshold, alternate stable states or irreversible change (Walker and Salt 2012). Scales are typically not isolated and will frequently be subject to feedbacks between larger and more local scales as well as fast and slow variables (Groffman et al. 2006). Planetary safe operating spaces have been proposed (Rockstrom et al. 2009) and might be defined for wildlife populations in accordance with abundance, composition and distribution thresholds that are associated with feedbacks within the population and with the supporting environment.

Thresholds can move and are difficult to quantify because of the involvement of multiple factors, non-linearity, diverse time and space scales and large response to small changes as a threshold is approached (Groffman et al. 2006, Walker and Salt 2012). Attempting to identify thresholds by experimental application of stress and monitoring for the beginning of change increases risks and has limited value because: (1) environmental quality may change, or with time, the condition of relationships that control processes, (2) changes in the relationships among controlling variables may render thresholds non-linear and surprising, (3) small stresses near thresholds cause relatively large changes (Scheffer et al. 2003) and (4) estimates of uncertainty are obliged to predict the state of ecosystems relative to an assumed threshold location (Clarke et al. 2001). Therefore thresholds may not be identified appropriately such that change from a desired state can be prevented. It is possible that the ability to clearly quantify a threshold indicates that the system is already at significant risk if not having already passed a threshold.

A safe operating space is intended to accommodate the variance expected to occur (1) within ecological systems and (2) from rapid increases in stress from external drivers due to changes in resource extraction. Defining a safe operating space may best address the cumulative effects of small changes that are most responsible for state change (Scheffer et al. 2001). Management can be directed to persistence of relationships, changes in ecological and population processes and states, and the unpredictability of the consequences of disturbance and change.

Resource extraction introduces novel disturbances and is subject to rapid increase in influence on ecological processes. Because of that managing industrial activity to remain distant from thresholds of safe operating space is justified. Resource extraction can cause a very rapid change in landscapes through access infrastructure (e.g. all-weather roads), surficial disturbance (surface mines, pipelines, well-sites), vegetation community change (e.g. clearcutting), land conversion (e.g. agriculture), or water allocation (e.g. agriculture, residential or industrial infrastructure). Thresholds that were met at earlier times may not persist. Conversely management of environmental resources to provide stable yield (e.g. annual allowable cut, animal unit months, and harvest rate) can compromise natural mechanisms that accommodate change (Groffman et al. 2006).

Governance commitment to safe operating space will be defined by responses to disturbance and change that cause approach to thresholds. Decisions may occur along a continuum from the near term benefit of resource extraction to the longer term benefit of the persistence of desirable ecosystem functions and services; and reflect synthesis of (i) the best determination of truth achieved by science, (ii) interest group perceptions and desires, and (iii) governance. Effective application of thresholds is expected to demonstrate the ability of this synthesis to meet obligations and challenges presented by resource utilization and development, and maintenance of ecological function, values and services, or to explain the willingness to accept suboptimal outcomes.

Governance

Ecological phenomena in emergent systems will progress independent of human perception, desires, beliefs, commitments or advocacy. However, these constructs will largely define societal intentions and activities regarding ecological values. Further, human understanding of ecological phenomena is dependent on human perception. The state and resilience associated with a resulting regime can be desirable or undesirable (Carpenter et al. 2001). Changing an undesired state requires overcoming the resilience, increasing the cost and decreasing the probability of success. Maintaining persistent native ecological communities and constituent populations obliges that human constructs (1) are based on the best scientific information, (2) are applied in an adaptive framework and (3) will accommodate and detect surprises (Lindenmeyer et al. 2010). Appropriate policy is needed to achieve these obligations. A clear understanding of what is desired to be resilient and to what, is needed to develop policies that enhance resilience (Biggs et al. 2012).

Policy development is inherently political so that success of enhancing resilience is a function of governance. Four principles of governance to enhance resilience have been proposed (Biggs et al. 2012) which provide a framework for testing:

(1) Participation by diverse interests may increase knowledge and cooperation, but participants focused on short term gains may hinder the achievement of resilience. Therefore a nuanced understanding of who participates and under what conditions is needed. Governance objectivity and commitment to achieve long-term resilient systems is required.
(2) Improve the understanding among scientists and managers of what complex adaptive systems are. Emphasize holistic rather than reductionist approaches. The emphasis needs to be on the use of adaptive approaches allowing for uncertainty rather than investing in monitoring and data collection without specific questions, rigorous methodology and adaptive capacity.
(3) Encourage participation in experimentation and monitoring to facilitate learning, which is expected to lead to improved governance, including a focus on questions regarding whether the management undertaken is the right course of action to perpetuate functions and how do we how what the right management and scientific questions are. The design of learning is critical as short term policies and objectives and power dynamics must be conducive to objectivity, collaboration, and long term efforts.
(4) Polycentric governance systems, with multiple governing authorities at different scales ought to be promoted. Polycentric governance provides modularity and functional redundancy, opportunities for enhanced learning and experimentation, and broader levels of participation.

Some properties of resilience are quantifiable but resilience can also be a metaphor for sustainability or system dynamics (Carpenter et al. 2001). These latter meanings may not be directly testable, but provide value as properties that can direct discussion that can stimulate productive hypotheses, and evolve governance structure (Hull 1988). Resilience science is striving to incorporate the properties and needs of governance with equal interest to that of ecological functions. Governance is crucial to achievement of resilience, but may be the aspect of resilience that requires the greatest development (Biggs. et al. 2012). Achieving the essential effective adaptive and precautionary management requires governance integrity (Doak et al. 2008) defined by the needs to maintain ecological function that allows for the persistence of ecological benefits.

Resilience is widely recognized as a valuable set of theories and management concepts applicable to ecological, social, and economic systems. Resilience strives to integrate these sometimes conflicting systems so that functions and benefits persist over extended times, or so that transformations are beneficial (Walker and Salt 2012). However, resilience approaches have had limited application likely due to a common governance focus on achieving maximum immediate benefits from resource exploitation. This governance focus ignores the true complexity of these systems (Allen et al. 2011) and separates the gain from exploitation from the costs of exploitation, a philosophy that is consistent with privatizing gains and socializing liability (Carney 2012). Resilience has achieved notable application to aquatic systems, tropical or semitropical climates and to some large mammals inhabiting marine or Arctic systems (SESMAD 2014). However application to temperate systems and in particular temperate large mammals is very limited (SESMAD 2014). Resilience is expected to result in a management system that is quite different from traditional wildlife management (Table 1.1. Allen et al. 2011). These elements of resilience focus on general rather than specific properties of systems, treating management actions as experiments and governance as policy options to be tested (Allen et al. 2011).

Summary

Demographics (vital rate effects on population processes) are essential to understanding population state. Achieving desired population or environmental state is dependent on accommodating ecological processes and complexity. Enhancing desirable resilience or overcoming undesired resilience requires a clear understanding of resilience of what to what (Carpenter et al. 2001, Biggs et al. 2012). Resilience concepts are expected to identify variables to be quantified and concepts to be explored by testing hypothesis. System structure and disturbances of interest need to be specified to assess the resilience of a system (Carpenter et al. 2001). Time and spatial scales need to be defined so that cross-scale significance (i.e. broad scale subsidy, self-generating correction) can be tested (Holling 1992), and the scope and nature of participation in governance framed (Biggs et al. 2012).

However, resilience management must be cognizant and accommodating of the tension between specific and general resilience. Specific resilience is the resilience of a specific part of the system to a specific shock. General resilience is the capacity of a system that allows it to absorb disturbances of all kinds (e.g. novel, unforeseen, and planned) so that the system continues to function as it had in the past (Walker and Salt 2012). For example, excessive focus on wolf (*Canis lupus*) predation on caribou (*Rangifer tarandus caribou)* or individual mortality of grizzly bears or ungulates inhibits emphasis on the management of landscape and wildlife community constituents that cause these vulnerabilities and increase the probability of a state change. Without this awareness, resilience may fall into the trap presented by focusing on the variability around equilibrium. A conceptual presentation of the adaptive cycle theorized for the system in question will provide context to understand findings.

Resilient Bighorn Sheep – Conceptual Project Design

To explore the requirements and benefits of a resiliency approach to management we propose a conceptual framework for a program focus on demography, genetics, horn growth, climate, and landscape change (Fig. 1.5). The program will attempt to: (1) measure the resilience of the bighorn sheep population in the Northern Rocky Mountains of Alberta and British Columbia; (2) identify climate and landscape conditions that affect this resilience; (3a) and present management options that will provide the governance and operational activities to achieve resilience and (3b) extend a resiliency approach to other values.

In our research program the demography of bighorn sheep is derived from abundance and composition surveys conducted over 40 years. The study area is divided into census zones without assumptions about population structure. Differences in composition and changes in abundance between census zones are assessed allowing inference of connectivity and scalar dependence. An associated study will attempt identification of biologically meaningful groupings of bighorns from migration, connectivity, and sex-specific movement detected from genetic analysis. These groupings in combination with demographic finding may define population units. The relationship between this focal scale of bighorn sheep census zones and the environment and management regime represents a social–ecological– system (SES).

The ecosystem elements that act as slow variables and the external drivers that influence slow variables will be examined by two associated studies. Identification of elements that enhance resilience supporting the bighorn population and those elements, in particular external drivers, that support resilience of an undesired state are the objectives. Mountain sheep horn growth offers a record of environmental conditions at the time of annuli growth, integrating variation in resource exploitation and bioenergetics costs associated with resource acquisition (Hik and Carey 2000). Variation in annuli growth will be used to assess the role of broad scale climate variability. Current and modelled future climate and landscape conditions are being developed to enable scenarios assessment of the risk of state changes and the opportunities and needs to enhance resilience.

Conservation programs for bighorn sheep must place a priority on preventing or controlling the influence of human-introduced disease, particularly disease carried by livestock (Cassirer and Sinclair 2006, Cahn et al. 2011, Besser et al. 2012). Fortunately, bighorn sheep in the Northern Rockies study area are not affected by these diseases at this time. Although original investigations regarding disease questions are not currently anticipated, we expect that management practices will be adopted to prevent the presence of domestic animals that may be disease vectors.

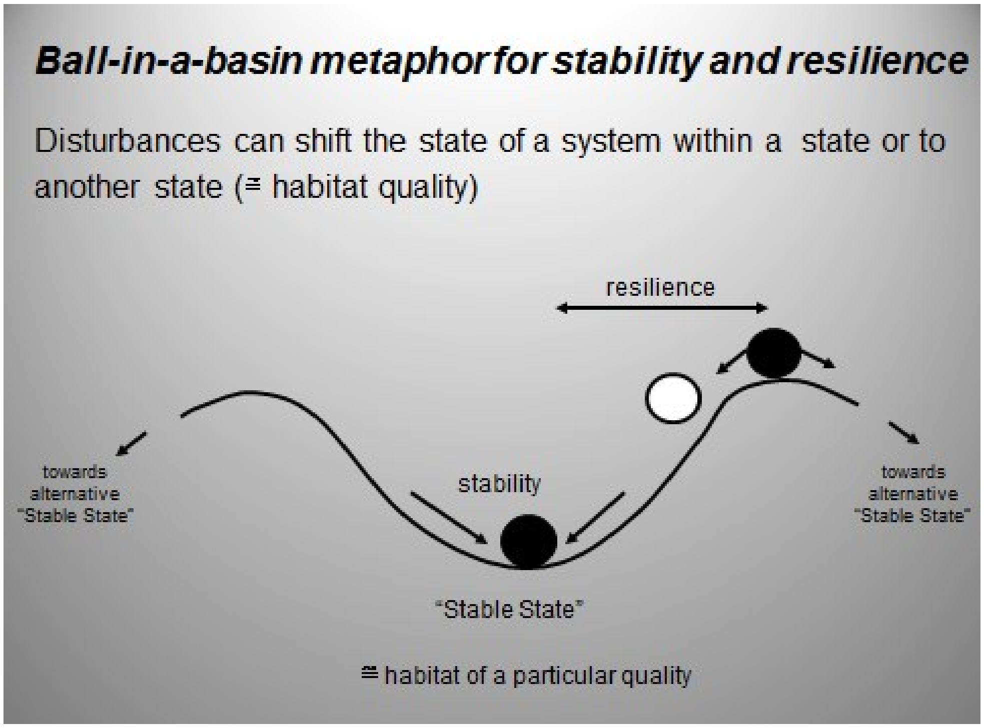
In the study area human-changes to the landscape are associated with high levels of selenium in the whole blood of bighorn sheep captured on coal mines beginning in 1999 and extending to 2014. We assess the levels of selenium detected in ungulate populations across western North America to determine an expected interval defining a safe operating space. A resilience approach to selenium management is warranted because the effects of selenium are subclinical and meaningful detection of the effects of high or low levels is difficult (Trumble and Sorenson 2008, Flueck 2012, Poppenga et al. 2012).

We propose to present a program with management hypotheses that test the application of resiliency concepts including: our estimated value of what defines a desirable state for target ecological values; our ability to determine and influence slow variables to achieve desired resilience; our ability to manage external drivers so that desired states can be achieved; and a governance structure intended to facilitate resiliency. We expect to develop a comprehensive monitoring program to test hypotheses and refine management. We of course understand that success at developing and testing these management hypotheses is dependent on holistic approaches that facilitate understanding of salient processes, properties and scales that determine evolved regimes. We do not anticipate pursuing reductionism “excessively.” We are pursuing improved understanding of how ecological systems perpetuate, and how human activities can be managed in a compatible manner. Our specific conservation purpose is to progress from quantification of presence and locations occupied by a population to identification and understanding of (i) the value of locations occupied, (ii) the variability of slow and fast variables, and (iii) surprises; and governance focused on how do we know what the right questions and actions are and what are the right questions and actions.

Table 1.1. Contrast between the elements of resilient wildlife management and a worst-case example of traditional management (From Allen et al. 2011).

Element of the system	Management	
	Traditional	Resilience
Species	Focus (icon emphasis)	Component (function emphasis)
Process	Implicit management goal	Explicit management goal
Structure	Conserved in its entirety	Selectively conserved
Management	Command and control	Adaptive
Scale	Single	Multiple
Uncertainty	Inhibited	Embraced
Variability	Inhibited	Embraced
Natural disturbances	Dampened where possible	Maintained where possible
Crisis	Calamity	Opportunity
Novelty	Suppressed	Encouraged
Redundancy	Low	High
Potential for learning	Low	High

Fig. 1.1. Relationship between stability and resiliency. The closer the state is to a threshold the greater the effect of a given disturbance (shock). The greater the environmental quality the better the ability to absorb a disturbance.(After Walker and Salt 2012)



Ball-in-a-basin metaphor for stability and resilience

Disturbances can shift the state of a system within a state or to another state (≅ habitat quality)

Fig 1.2. Ecological resilience and alternate stable states. Relationships of ecological resilience (existence of function) to (1) engineered resilence (efficiency of function) and (2) the influence of environmental quality on variation in resilience within a state, and the potential to shift to an alternate stable state. High resilence provides tolerance to disturbance and maintains the state. Low resilience provides limited tolerance to disturbance,and small amounts of stress may cause an abrupt change in stable state.

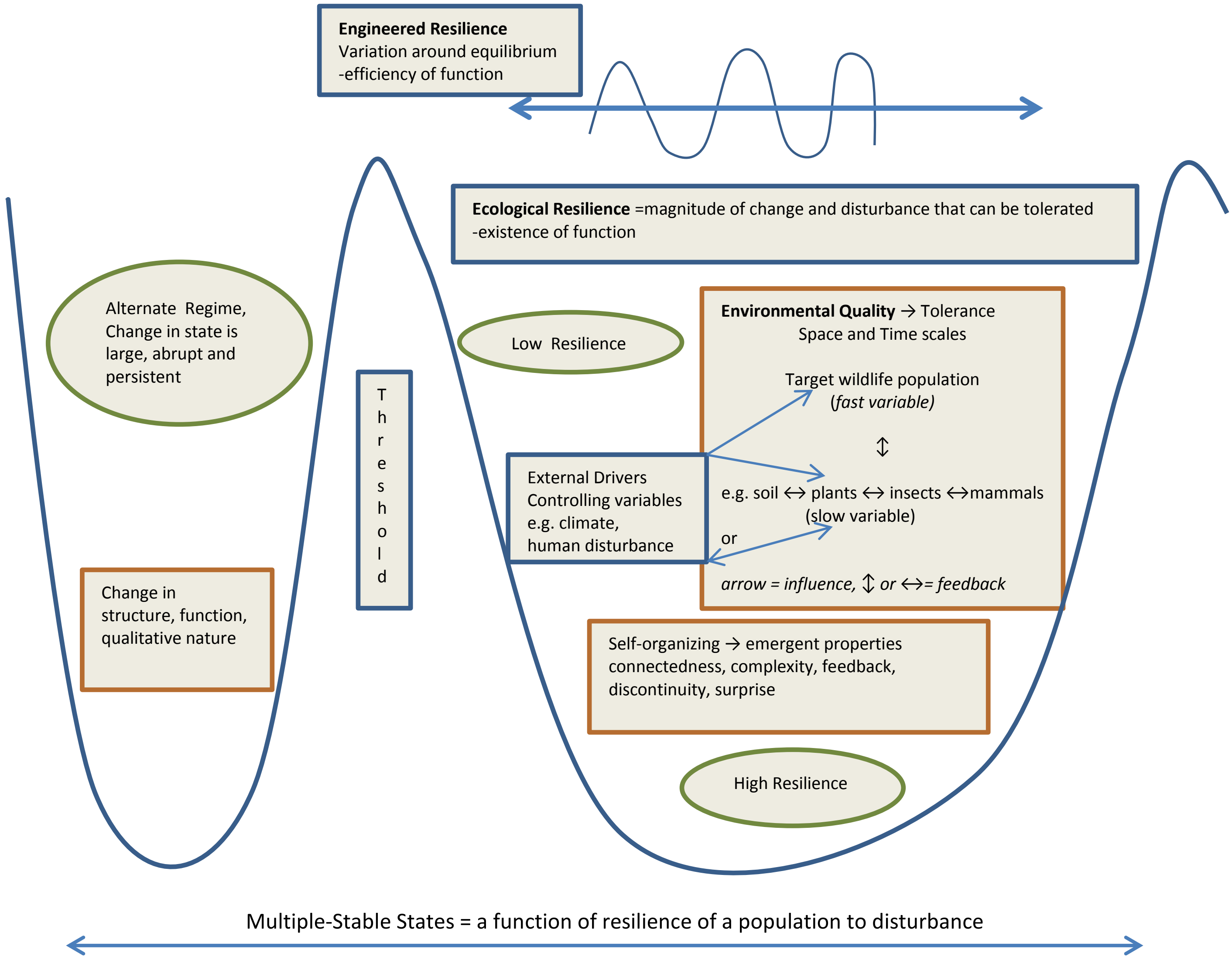
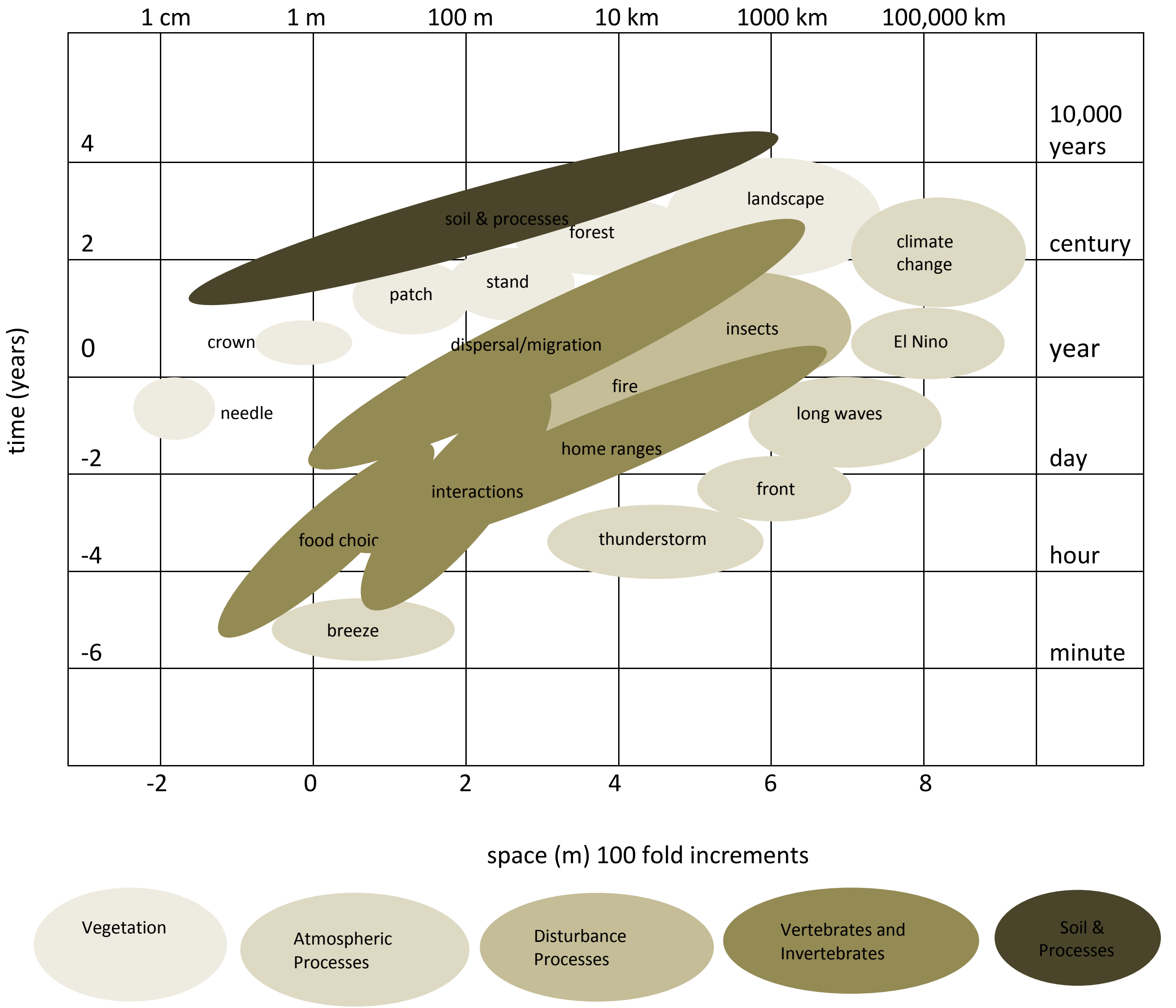
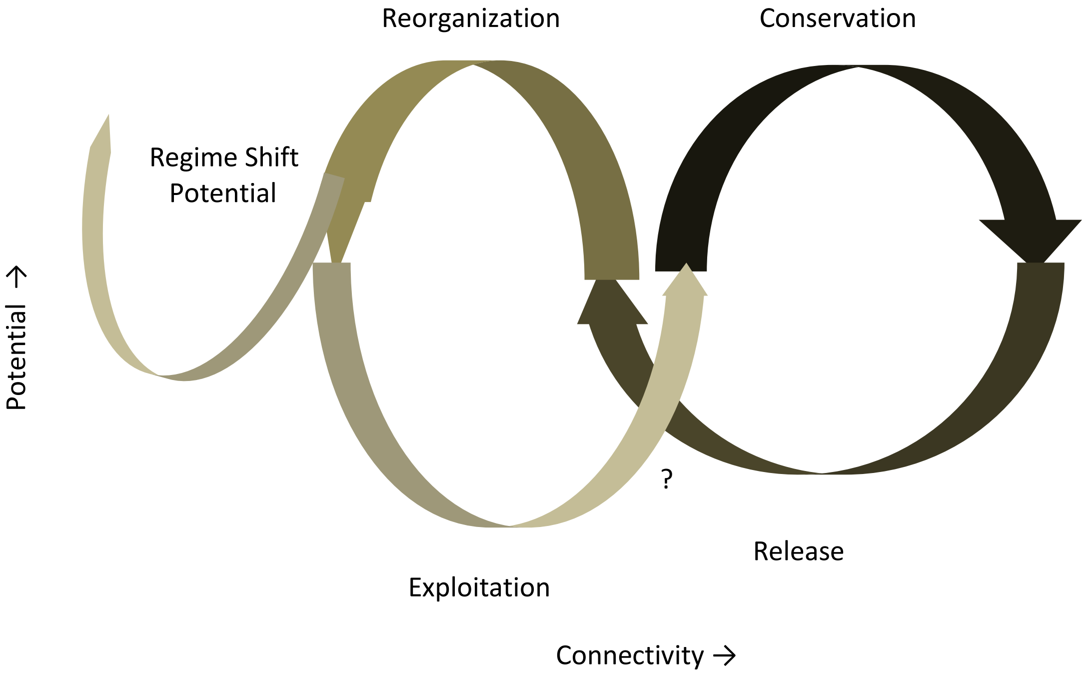


Fig. 1.3. Time and space scales of boreal forest soil, vegetation, atmospheric and two disturbance processes, and animal movement. Scales, structures, processes and biota are interconnected. Vegetation and topographic structure support biotic elements that provide diversity and redundancy. (Adapted from Gunderson and Holling 2002; interactions and soil added)



Time and space scales of the boreal forest (Holling 1986), of the atmosphere (Clark 1985), and of their relationship to some of the processes that structure the forest. Contagious meso-scale disturbance processes such as insect outbreaks and fire mediate the interaction between faster atmospheric processes and slower vegetation and soil processes. Scales at which vertebrates and invertebrates choose food items, occupy a home range, disperse and move in response to interactions with conspecifics or other species vary with their body size (Holling 1992)(cited and quoted from Gunderson and Holling 2002 fig. p-1).

Fig. 1.4 . Adaptive Cycle (adapted from Gunderson and Holling 2002) showing the relationship among of the four ecosystem functions of exploitation, conservation, release and reorganization that sustains a regime and the potential for regime change.

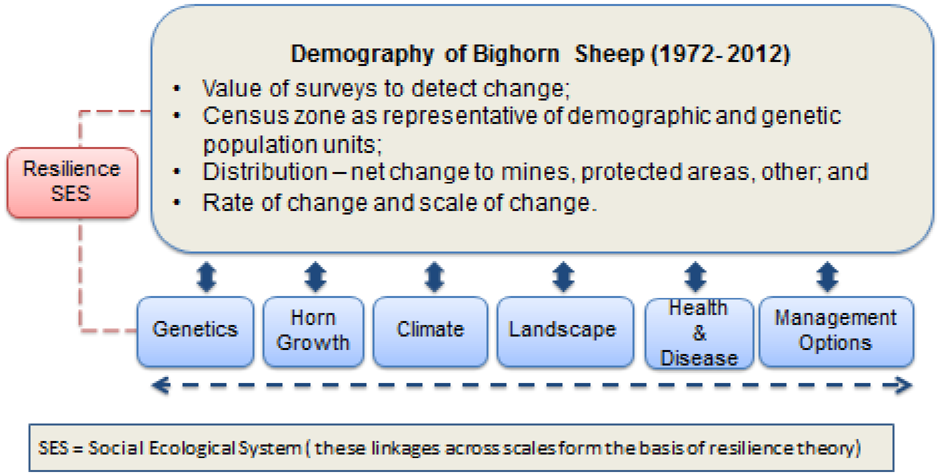


? = Is the potential that reorganization will result in a regime shift by processes in the reorganization phase increased by (i) an increase in the rates (frequency or magnitude) of release events, (ii) the occurrence of release events early in or prior to the conservation phase, or (iii) release events of a non-evolutionary nature.

(Quoted from Gunderson and Holling 2002) “A stylized representation of the four ecosystem functions and the flow of events among them. The cycle reflects changes in two properties: (1) y axis, the potential inherent in the accumulated resources of biomass and nutrients; and (2) x axis, the degree of connectedness among controlling variables. The exit from the cycle, indicated at the left of the figure suggests, in a stylized way, the stage where the potential can leak away and where a flip into a less productive and organized system is most likely (Holling 1986).”

Fig. 1.5 *Resilient Bighorn Sheep Project - Overall Conceptual Framework*

Framework components and the relationship to demography and the social ecological system.



Demography of Bighorn Sheep (1972-2012)

- Value of surveys to detect change;
- Census zone as representative of demographic and genetic population units;
- Distribution – net change to mines, protected areas, other; and
- Rate of change and scale of change.

SES = Social Ecological System (these linkages across scales form the basis of resilience theory)

Chapter 2

Resilient Space: Bighorn Sheep *(Ovis canadensis)* Demographics, Resilience and Response to a Novel Habitat in the Northern Rocky Mountains

Introduction

Population distribution among a mosaic of habitats of differing quality transfers demographic attributes across space (Murphy 2001), influencing ecological resilience, and either benefiting or diminishing population vigour (e.g. Biggs et al. 2012). Demography, vital rate influence on population processes (Boyce et al. 2006), is fundamental for the application of ecological theory to management (Pulliam et al. 2011); achieving resiliencies and disturbance regimes that contribute to persistence of native species and ecosystems (Allen and Hollings 2008, Walker and Salt 2012); conservation planning to address expected human induced changes to environmental variability (Boyce et al. 2006); and detecting and accommodating surprises (Lindenmayer et al. 2010). We investigate the demographics of bighorn sheep (*Ovis Canadensis*), a large bodied mobile species, that occupy a complex ecosystem where pre-Anthropocene (Holocene epoch) population and habitat function may persist, to better understand environmental quality, population vigour, and accommodation of uncertainty associated with self-organization following disturbance.

We examined bighorn sheep demographics over 40 years on a 42,000 km^2 study area in the northern Rocky Mountains, the northern extent of the species occurrence (Fig. 2.1). Abundance and composition are relatively obtainable metrics for species such as bighorn sheep that occupy open habitats and have horn shapes that enable age and sex class determinations. Population abundance in the northern Rockies is at least an order of magnitude greater than other bighorn sheep populations that have been studied in North America. Bighorn sheep habitats in the northern Rockies are contiguous or closely proximate, possibly enabling distribution, including long distance movement. Population size and geographic scope is expected to enable multi-scalar relationships. This complexity may identify connectedness, relationships and processes controlling resilience. Variables that control bighorn sheep abundance and productivity in the northern Rockies may be different than that inferred from the relatively small scale geographic range and population abundance of bighorn sheep typically investigated in North America. Migration, connectivity and sex specific movement of bighorn sheep may be detected from genetic analysis conducted by companion studies. We are specifically interested in how populations in the northern Rockies change with time, and is resilience related to productivity and population structure on native range compared with novel range. We explore managing for ecological resilience, accommodating surprises, and assessing habitat quality.

Ecological resilience is concerned with the persistence of function and the existence of alternate states that result from the environmental quality generated by ecological patterns and processes governing ecosystem and population self-organization following disturbance (Holling 1973, Holling 1986, Carpenter et al. 2001, Cumming et al. 2008, Walker and Salt 2012). The adaptive capacity or magnitude of disturbance and change that an ecosystem or population can tolerate without changing self-organizing processes and structures measures resilience (Holling 1973, Holling 1986, Gunderson 2000, Carpenter et al. 2001). Retention of functions, feedbacks, structure and identity (Walker et al. 2004) perpetuate patterns and processes. Self-organizing processes and structures are maintained by persistent relationships among ecological components and scales, which in turn are influenced by an appropriate degree of connectedness (complexity) (Holling 1973, Holling 1986, Gunderson and Allen 2010, Curtin and Parker 2014). Changes in self-organization may cause a shift to an alternate stable state, which may occur in a surprising and discontinuous manner (Holling 1973, Gunderson and Allen 2010, Lindenmayer 2010).

Detecting and analyzing surprises or unexpected findings are critically important to advancing ecological understanding and natural resource management (Doak et al. 2008, Lindenmayer et al. 2010). Surprises are common and may become increasingly frequent consequences of “interacting environmental stressors” such as climate change and land use (Lindenmayer et al. 2010) and increasing environmental variability (Boyce et al. 2006). Emergent properties characteristic of self-organizing systems and insufficient knowledge of ecosystem function (Holling 1973, Doak et al. 2008, Lindenmayer et al. 2010, Curtin and Parker 2014) magnify uncertainty, heightening the importance for conservation plans to accommodate surprises.

The source and demographics of animals at a location (habitat) define habitat quality (Van horn 1983, Pulliam 1988, Schlaepfer et al. 2002, Bock and Jones 2004, Pulliam et al. 2011) and the potential for a shift to an alternate ecological state (Walker and Salt 2012). The relationships of demographic measures to habitat quality are better understood and should be emphasized, but distribution will be revealing and greater understandings for effects on population persistence should be pursued (Johnson 2007). Productivity and distribution processes produce a continuum of sources and sinks respectively exporting or consuming animals (Thomas and Kunin 1999, Mills 2007). Sinks are net importers of animals, may display notable increases in animals, have limited ability to support imported animals and in the most severe cases are attractive and detrimental to some species (Pulliam 1988, Donovan and Thompson 2001, Delibes et al. 2001, Battin 2004). This attraction can cause habitat area (realized niche) to be greater than the source area of resources and productivity (fundamental niche) that sustain a population (Pulliam 1988, Hull et al. 2011). Habitat quality is the ability of the habitat to support population growth and persistence (Krausman 1999, Garshelis 2000, Gaillard et al. 2010) and identifies the management obligation to sustain, enhance, or counter the resilience that maintains the state.

Habitat is the place an organism lives (Thomas 1978, McComb 2008) without regard to the value of occupation. Habitat selection, particularly of human altered habitats cannot be assumed to predict habitat quality (Hobbs et al. 2009, Sih et al. 2011, Sih 2013). Habitat selection may not advantage or relate to demographic processes, population performance or health of individuals (Van Horne 1983; Pulliam 1988, Bock and Jones 2004, McShea 2005, Nielsen et al. 2006, Johnson and Seip 2008). Nor is abundance alone informative of the source or vigour of a population (Van Horne 1983, Johnson 2007, Mills 2007). Changes in occupancy may be due to changes in abundance or distribution or both.

The state of a population is described by abundance, composition and distribution within and among spatial scales occupied by discreet demographic groups (Bock and Jones 2004, Bender 2006, Boyce et al. 2006) or genetic aggregations (Hampton et al. 2004, Palsboll et al. 2006, Estes-Zumpf et al. 2010, Lowe and Allendorf 2010). Demographic and genetic populations may occur at the same or different spatial scales (Esler et al. 2006, Mills 2007). Processes of disturbance and regeneration continually stress ecosystems and the state of associated populations (Holling 1973, Holling 1986, Carpenter et al. 2001, Scheffer et al. 2001, Folk et al. 2004, Biggs et al. 2012, Curtin and Parker 2014). Population processes of birth, death, immigration and emigration, the only ways animals may enter or leave a population, may be affected (Pulliam 1988, Thomas and Kunin 1999, Mills 2007). Asymmetry between productivity (birth and death) and changes in abundance may indicate the influence of distribution (immigration or emigration) on species presence.

Our hypothesis is that bighorn sheep productivity (females as a proportion of adults, lambs as a proportion of total bighorn sheep abundance) is the appropriate measure of fitness defining population vigour and habitat quality, and that population connectivity among habitat variations across a broad landscape contributes to the adaptive capacity that controls ecological resilience. We predict that knowledge of productivity and broad scale distribution will enable identification of a safe operating space (*sensu* Rockstrom et al. 2009), determining limits if the system is to persist. We predict that the numerical response of bighorn sheep does not consistently reflect fitness, and does not measure environmental (habitat) quality. Resilience at source habitats is also predicted to maintain local bighorn sheep presence (smaller scale) and cumulatively determine demographic population persistence (larger focal scale).

We use abundance and composition from a time series of bighorn sheep censuses to demonstrate the vigour of populations and the quality of habitat within a series of census zones. Dimorphic, polygynous ungulate populations are characterized by female biased sex ratios. These ratios persist whether hunting occurs or not (McCullough 1999) and appear to result from a complex of interacting factors for which the ultimate causes are difficult to discern, although higher rates of male mortality (e.g. Jorgenson et al. 1997) are common (see reviews by McCullough 1999, Berger and Gompper 1999, Hoffman and Genoways 2012, Blank and Yang 2013). However, selection for increased female survival could contribute to female skewed sex ratios in polygynous species (Haridas et al. 2014). Female skewed sex ratio can be viewed as active sexual selection that increases fitness (McCullough 1999). Modeling experiments also indicate that differences between sexes in predisposition to disperse or density-dependent response, and polygynous mating systems increase the dynamics in spatially structured populations, including affecting adult sex ratio (Ranta et al. 1999).

Bighorn sheep and other single birth species have a low intrinsic rate of increase. Female biased sex ratios are necessary to provide recruitment that can sustain a population and possibly to advantage from periods of better bioenergetics of resource utilization. Female skewed composition may allow greater population abundance and reproductive potential when resources are constant or resource overlap between the sexes is high (McCullough 1999). If resource overlap between sexes is small the population dynamics of each sex is expected to be a function of their respective abundances (Mysterud et al. 2002) and resource segregation may allow greater increases in female abundance (McCullough 1999).

Study Area

Description

The study area (Fig. 2.1) extends from the northern extent of bighorn sheep species range, located in the headwaters of the Torrens (Alberta) and the Narraway (British Columbia) rivers, south through Alberta, including National Parks, to the headwaters of the Red Deer River. Bighorn sheep are not present to the west and north, and presence east of the study area is limited to Ram Mountain, a demographic isolate (< 200 individuals) adjacent to the Clearwater census zone (Fig. 2.1), where bighorn sheep have been individually marked (~95%) and studied since the early 1970s. Ram Mountain bighorn sheep exhibit genetic connection through rams from the study area (D.Coltman Per. Comm.). Bighorn sheep movement presumably occurs in Alberta across the southern boundary of the study area to the Bow River drainage, which allows connection to bighorn sheep in British Columbia's Kootenay River drainage. However bighorn sheep abundance is relatively low in the Wildlife Management Unit (WMU) that is southernmost in the study area (WMU 416) and the WMU immediately south of the study area (WMU 414). In eight winter surveys from 1986–2009, an average of 30 adult bighorn sheep were observed in each of these WMUs (WMU 416: range 6–83, area=232 km^2) (WMU 414: range 8–63, area = 436 km^2). There is no measured or anecdotal evidence of large movements of bighorn sheep over the two boundary WMUs, although 159 adult bighorn sheep were observed in WMU 416 in winter 2011 (unpub. Alberta Environment and Parks (AEP) data). Bighorn sheep presence in Banff National Park (BNP) is concentrated adjacent to the west boundary of the Clearwater census zone and total bighorn sheep abundance has been stable from 1986 to 2011 (BNP data,) although composition variability cannot be assessed. Therefore, there is little likelihood that emigration or immigration via the southern boundary will affect bighorn sheep population dynamics in the study area.

Bighorn sheep within the study area are not known to have diseases, such as pneumonia (*Pasteurelleae spp., Mycoplasma spp.*), which commonly regulate and limit bighorn sheep populations throughout southern Canada and the United States (Besser et al. 2012, Cahn et al. 2011, Cassirer and Sinclair 2006). The study area is relatively intact, with anthropogenic change limited to transportation corridors through national parks (Highway 16 and 93, Canadian National Railways mainline paralleling Highway 16), the townsite of Jasper, recreational infrastructure at Miette Hot springs and surface coal mining within the Cadomin (L&GR census zone) and Willmore census zones.

Disturbance management in the Northern Rockies includes lands that are managed for (1) wilderness, (2) transportation corridors within national parks, (3) multiple-use subject to limited intentional disturbance and (4) intensive resource extraction by surface mining with a residue of poorly understood novel landscapes resulting from human activity. Hunting is permitted on most provincial lands managed as multiple use or wilderness. Hunting is prohibited on lands subject to intensive resource extraction, and some wilderness lands, including all of Jasper and Banff national parks.

Census Zones

Census zones (Fig. 2.1) are determined by the location of major rivers (Red Deer, North Saskatchewan, Brazeau), jurisdictional boundaries of lands administered provincially (Alberta AEP Regions) or federally (national park boundaries) and the surface mineral lease boundaries of the Luscar-Gregg River Mines (L&GR) complex which is characterized by novel range. Demographic (changes in bighorn sheep in a census zone does not affect bighorn sheep in another census zone) or genetic (low rates of gene flow between census zones) (Iverson et al. 2004, Lowe and Allendorf 2010) population assumptions are not assigned to census zones. However, historically, census zones have been assumed to be population units that are measured by surveys and managed as separate population units. Census zones extending from the north are designated as: Willmore, Jasper, Cadomin, L&GR, Nordegg, Clearwater and North Banff.

Methods

Survey Methods

Native ecological communities on provincial or national park lands were surveyed by air to obtain composition and minimum count population estimates on identified winter ranges from late January to early March. Survey frequency for any winter range varies from biannually to up to a six year separation because of snow or wind conditions. Methodology is consistent with other jurisdictions in Western North America (British Columbia 2002, Colorado 2009, Idaho 2010, Montana 2010, Nevada 2001, Oregon 2003, South Dakota 2007, and Utah 2008) and reflects appropriateness of information obtained and the logistical considerations of bighorn sheep range. A Bell 206 jet ranger helicopter, with a navigator-classifier in the front left seat beside the pilot and two observer- recorders in the backseat, systematically reconnoiter winter range from the air to locate groups of bighorn sheep, which will almost always employ the escape strategy of running in a line or fan along ridges and plateaus. The helicopter approaches the line from the rear and flies towards the front, classifying to ewe, lamb, ¼ curl ram, ½ curl ram, ¾ curl ram, or legal ram (4/5 curl). Pursuit time is minimized, and may total $\leq$ 10 seconds for small groups (e.g. six bighorn sheep) with easy to identify composition, but may extend to ~60 seconds for large (e.g. >30 bighorn sheep) groups that bunch up, turn back or break into several lines going different directions. Pursuit is terminated if bighorn sheep flounder in snow, labour in warm temperatures, or after the second classification attempt. Unclassified animals are categorized as unclassified bighorn sheep or unclassified rams. Surveys of novel range on coal mines in WMU 446 in the Willmore used the same methods. All surveys were conducted by Alberta Government or National Parks staff, except those for the L&GR.

Pre-rut abundance and composition data from novel range on the L&GR was obtained from regulatory submissions by the succession of mine operators to AEP, or predecessors. Useful pre-rut data is available for the September to mid-October period of each year from 1994 to 2011. Estimates of the number of ewes, lambs, yearling rams and ewes, and four horn size classes of rams are the highest single day presence of each class of bighorn sheep from up to six surveys in each pre-rut. Winter abundance and composition data was collected from ground surveys by contractors for the mine operator, in those years when the province conducted aerial surveys on adjacent native range. All L&GR data has been collected by the same contractor.

Data analysis

An abundance measure for each census zone was achieved by pooling classification data for all winter ranges in the census zone for each survey year. North Banff was excluded because composition could not be corroborated. Statistical analysis was conducted by Minitab version 16 statistical software (Minitab ® Copywrite ©2012 Minitab Inc.). Annual abundance measurements for each sex on each census zone from 1982–2011 were tested for normal distribution. Outliers of high or low abundance measures were identified by testing for unusual observations of fit or residual, where the residual of the annual measurement is >2 or <-2 times the standard deviation of the residual for all survey years in that census zone (standardized residual >2 or <-2) (e_i *=residual difference between observed and predicted value/ standard deviation of the residual)*. After an outlier was identified and excluded, data from the remaining years was again tested until no further outliers were identified. Determination of changes in abundance for each census zone for each sex-time period excluded rams, ewes or both sexes in those survey years where unusual observations of fit or residual were identified, unless otherwise stated. In Nordegg, the 1982 abundance measures for both ewes and rams were excluded, so the 1980 abundance measures were used as the point estimate for 1982. Measurements of bighorn sheep abundance with large standardized residuals are true counts of the rams or ewes observed on the census zone in that year, but deviate significantly from expected measures over the time series. Measured high abundances of rams or ewes that were excluded as outliers are believed to be year event differences in distribution that increased the abundance of one or both sexes in specific census zones, and are dealt with as such in results. Low abundance results from partial surveys due to weather or other constraints.

Unusual observation of rams in the L&GR in 2008 (standardized residual =2.2) was not excluded because the apparent lack of movement from the pre-rut 2007 survey provided bias against our connectivity hypothesis (Supplemental Fig. 8). Observation of rams in 1988 and ewes in 1982 on L&GR were both identified as having large standardized residuals, but were not excluded. These are measures of abundance prior to distributional change and accurately reflect changes in abundance over time.

Fitted line plots for each sex for each of the 6 census zones (North Banff excluded) for 1982–2012 were generated with polynomial regressions, producing twelve sex-census zone pairs. Significant changes for five sex-census zone pairs were identified, all with linear regression as the best fit. Non-linear fit (quadratic or cubic function) for the other seven sex-census zone pairs resulted from non-significant trend with non-significant inter-survey variation. To achieve the objective of identifying changes in abundance of rams and ewes over the time series, comply with the finding of linear regression as the best fit for significant change, and to achieve a common comparison, linear regression was conducted for all twelve sex-census zone pairs.

All surveys from 1972–2012 were acceptable for determining composition because an estimated 40-90% of bighorn sheep in a census zone were observed during a survey. This estimate was determined from (1) comparison of bighorn sheep observed during aerial survey versus the known marked population at Ram Mountain (~70%), a complex deemed difficult to survey from the air (J. Jorgenson per.comm.), and (2) interpretation from differences in the number of animals observed among survey years (e.g. Fig. 2.3; result for a low yr. / (result for a high yr. /0.7)), after eliminating extreme results due to partial surveys. The Ram Mountain estimate of 70% is considered conservative and consistent with the 66% probability of locating instrumented bighorn sheep on ranges in Oregon (Taylor et al. 2002) and

Idaho (Bodie et al. 1995) where observation of bighorn sheep is difficult. Bighorn sheep in the Northern Rockies occupy open slopes and plateaus in alpine habitat and run when disturbed, suggesting higher rates of observation than bighorn sheep in the Ram Mountain, Oregon or Idaho situations. Sightability estimates of 0.75 to 0.81 (George et al. 1996) and 0.82 ±0.072 SD (Poole 2010) may be more appropriate for the alpine habitats in our study area.

Bighorn sheep classified as yearling rams and ewes in the L&GR were respectively grouped with rams and ewes greater than 1.0 years of age to standardize measurement with classifications obtained from the aerial surveys. Identification of yearlings can only be accurate where bighorn sheep can be closely approached on the ground and observers can be confident that almost all bighorn sheep are observable. Yearling identification requires open, high visibility, highly trafficable landscapes, occupied by animals habituated to human presence. These conditions are rarely present on bighorn sheep range. Where animals are easily accessible or habituated, tree cover often affects visibility and confidence in the proportion of animals observed. Measurements, particularly productivity measures, from ranges such as L&GR and from intensively marked populations such as Ram Mountain and Sheep River, need to be standardized with data that can be obtained on typical bighorn sheep ranges. However, the ability to identify yearlings does facilitate estimating annual survival.

Productivity measures, of (1) ewes as a proportion of adults, (2) lambs as a proportion of the total bighorn sheep abundance and (3) the lamb: ewe ratio, were derived from composition. Large standardized residuals were restricted to the period before 1980, except for one survey in the WMU 438 portion of the Cadomin census zone. Inclusion of this WMU 438 data resulted in a more conservative assessment of the high productivity on native range relative to L&GR (i.e. outlier is a low productivity estimate on native range). The Cadomin census zone was separated into the constituents, WMU 437 and WMU 438, to enable a finer scale assessment of productivity relative to L&GR. Potential (ewes as %

of adults) and realized (lambs as % of total bighorn sheep) productivity from 1972–2011 for each census zone was assessed relative to the respective standards of 65% ewes and 20% lambs (Fig. 2.5a).

Because bighorn sheep were not classified in the 1983 survey of Jasper, we estimated parameters complying with the 95% confidence interval, determined from all surveys on the five native range census zones (including the 4 classified surveys from Jasper) for the 3 interdependent variables of (1) ram: ewe: lamb, (2) ram: ewe as a proportion of adults and (3) lamb: ewe ratio. The number of rams and ewes observed in the 1987 Jasper survey were within the 95% CI calculated for Jasper 1983, and assumed as the point estimates for Jasper 1983 rams and ewes. Thus assuming there is no change in ram or ewe presence between 1983 and 1987. Lamb presence in Jasper in 1983 which is estimated as a function of total bighorn sheep observed less estimated adults is at the upper end of the 95% CI. However this method reduces the estimated adult abundance in 1983 resulting in a more conservative assessment (bias against) of the decline in adults in Jasper from 1982–2012.

Animal movement data within the study area does not exist. The influences of productivity (births-deaths) and distribution (emigration and/or immigration), the only ways by which individuals can move into or out of a population, on changes in abundance on the L&GR census zone can be assessed. As a fundamental step in validating our hypothesis the changes in abundance, the adult sex ratio and proportion of lambs present in respective census zones over the time series of surveys are used to test the claims that L&GR productivity is greater than or equal to productivity on native range.

Results

Abundance

At the northern Rockies focal scale, stable abundance and sex composition of adult bighorn sheep from 1982/83 to 2011 was demonstrated by the available three years of Jasper survey data combined with data collected on provincial lands in closely proximate years (Fig.2.2, Table 2.1, Supplemental Table

1a); corroborated by regression of the 1982–2012 time-series of surveys (large standardized residuals excluded) (Fig. 2.3, Table 2.2) and mass balance of six census zones (Fig. 2.4). The Jasper 2011 survey results are corroborated by the 2012 survey results (Fig. 2.3) and subsequent 2013 and 2015 surveys (AEP unpublished data). The sample years of 1982, 1987 and 2011 are respectively prior to, at the outset of and at the peak of bighorn sheep increase in abundance on L&GR. Ram and ewe abundance and female skewed adult sex ratio at the northern Rockies scale remained constant as increased abundance with a balanced sex ratio on novel range of L&GR progressed. The increase in ram and ewe abundance on L&GR respectively are inversely correlated with change in ram abundance on all native ranges ($r = -0.998$, $p = 0.043$) and change in ewe abundance on native range most proximate to L&GR in Jasper ($r = -0.998$, $p = 0.040$) or Jasper and Cadomin combined ($r = -0.992$, $p = 0.078$). The small sample size of Jasper survey years inhibits determination of probability.

At the finer scale of the census zone, changes have occurred in both ram and ewe abundance and composition from 1982–2012 (Fig. 2.3 & 2.4, Table 2.2). These changes are asymmetrical between sexes in the three native range census zones most distant from L&GR (Fig. 2.3, Table 2.2) and declines in ewe abundance are greater than declines in ram abundance in the two census zones most proximate to L&GR (Fig. 2.4). Population substructure in years absent of Jasper survey data is consistent with the three years that Jasper survey data is available (Fig. 2.3). This more frequent sampling corroborates the stable adult abundance and sex ratio from 1982-2011 at the northern Rockies scale and the sex specific difference in geographic influence on the inverse correlation of changes in abundance between native range and L&GR. Of note, in Nordegg the decrease in ewes in 2011 (Fig. 2.4) is a year event contrary to the non-significant increase in abundance (Table 2.2b).

Changes in abundance at the finer scale of the census zone from 1982 to 2011 (Fig. 2.3) are consistent with net flow of both sexes from native range to novel range (Fig. 2.4). This flow may be structured by differences between sexes in predisposition to distribute and possible independence of ewes by distance. Rams exhibited a pattern of decreasing abundance on all five native range census zones, including a significant decrease of >25% in Jasper (df=3, t=-10.8, p=0.008) and approaching a significant decrease in Cadomin (df=8, t=-2.14, p=0.07) (Table 2.2a). The one novel range exhibits an absolute and significant increase in rams (df=9, t=11.97, p <0.001)(Table 2.2a), which exceeded by an estimated 58 rams the total decline from all five native range census zones (Fig. 2.4).The Increased abundance of rams on L&GR captures the cumulative effects of the gradual, and in most census zones statistically insignificant, decline in ram abundance on native range. From 1982–2011 the abundance of ewes (Table 2.2b) increased significantly by >20% in Clearwater (df=11, t=2.35, p=0.04) and was stable in Nordegg (df=12, t=0.34, p=0.742), and Willmore (df=6, t=0.86, p=0.432), although the observed ewe abundance continued to increase. Ewe abundance decreased significantly by >45% in Jasper (df=3, t=-9.43, p=0.011) and was stable in Cadomin (df=8, t=-1.16, p=0.286), but declined by >20% in WMU 438 post-1994 (Fig. 2.3), consistent with distribution change to the adjacent L&GR. The increase in ewe abundance on L&GR (d= +359) from 1982-2011 (df=9, t=12.44, p <0.001) (Table 2.2b) equals the estimated decline in the number of ewes from Jasper (Fig. 2.4). The three census zones exhibiting stable or increased abundance of ewes were the farthest from novel range, while the two census zones exhibiting the largest decline in both ewes and rams are in close proximity to the novel range (Fig. 2.1).

The northern Rockies adult cohort observed in late winter 2011 on winter ranges surveyed from 1972 to 2012 is estimated at 1273 rams and 2336 ewes, consisting of 65% ewes (df=2, X^2=2.799, p= 0.247, Table 2.1), an insignificant change in abundance and composition from 1982/83 (Fig. 2.2). Northern Rockies abundance estimates for the period prior to 1982 are precluded because of the absence of data from Jasper for 1972–1982, and provincial data from years proximate to the 1967 Jasper survey. Within the entire 42,000 km^2 Northern Rockies study area, an estimated $\leq$500 adult bighorn sheep are not included in the analysis because historical and/or current population data is lacking for ranges occupied by these animals (Supplemental note 1). This exclusion is not expected to change results generated from the 3609 adults included in the analysis.

Population abundance and composition stability from 1972 to 2011 is suggested by the rate of change (($\tilde{\lambda}$) estimates in 1972–1980 for both rams and ewes (Table 2.3). The estimated annual rate of change ($\tilde{\lambda}$) in the number of rams and ewes for 1978–1980 and 1972 –1980 is occasionally stable (three out of 16 sex-time periods) but predominately high (10 out of 16 sex-time periods $\geq$ 1.06) and biologically unrealistic over the multiple consecutive years of most survey intervals, suggesting the low observation of bighorn sheep in 1972–1978 reflects a period of learning how to survey bighorn sheep rather than a period of lower bighorn sheep abundance. The discontinuity in estimated rate of population change between pre- and post- 1980 is corroborated by disagreement between estimated population trend and magnitude from 1972–2012 relative to 1980–2012 or 1982–2012 (Table 2.2, Supplemental note 2).

Unexpected high abundance (residual of abundance is >2 X standardized residual of the 1982–2011 series of abundance measurements for that census zone) of both rams and ewes occurred in the Nordegg in the years 1982, 1993 and 2001, non-consecutive survey years, separated by four and three surveys respectively. High abundance of rams and ewes was observed in Clearwater in 1993, and rams in 2009. These occurrences suggest year events involving distribution changes for bighorn sheep that also occupy Banff or the Brazeau-Southesk bighorn sheep range (>400 bighorn sheep present in four winter surveys 1983-2012) in Jasper. Low abundance of ewes in Clearwater in 1988 and 2003 (standardized residual >2) reflected the year's partial survey.

Productivity

Productivity measures, determined from the composition of bighorn sheep, corroborate that change in census zone abundance results from distributional changes. The increase in both rams and ewes on novel range of L&GR (Fig. 2.3, 2.4,) is not internally generated. Ewes as a proportion of adults (ANOVA: $F_{7, 105}$=28.1, r^2= 65.2, p<0.001) is the primary determinant of productivity, and along with lambs as a proportion of total bighorn sheep (ANOVA: $F_{7, 105}$=2.73, r^2=15.4%, p=0.011), are not different among native range census zones. But both productivity measures are significantly greater on native range than on the novel range of L&GR at both the pre-rut and winter time periods (Fig. 2.5b). WMU 437 in the Cadomin has a lower ewe proportion than other native range (ANOVA: $F_{5, 77}$ =15.59, r^2=50.3%, p<0.01), but not a lower lamb proportion (Fig. 2.5b), suggesting a pseudo-sink.

Ewes range from 60-70% of adults, concentrating at ~65% on native ranges (Fig. 2.5a & 2.5b,) consistent with expectations for natural sex ratios and population persistence in ungulates (see Clutton-Brock et al. 1982, Clutton-Brock & Lonergan 1994, Boukal et al. 2008, Weaver and Weckerly 2011, DeCesare et al. 2012). Lambs averaged 18-22% of the population over an extended number of years, consistent with expectations in Alberta (AEP 2015). Lamb presence ranged from 10-27% of bighorns in a native range census zone in any given year, although lamb presence of less than 17% in a winter is uncommon on native ranges (14/84 census zone winter surveys and concentrated in Nordegg and Clearwater) (Fig. 2.5b).

The lamb: ewe ratio is not significantly different among any of the census zones (one-way ANOVA: $F_{7, 105}$ =1.10, r^2=6.8%, p=0.368). However, the highest absolute lamb: ewe ratio at 0.49 and 0.48 occurred respectively in the WMU 437 and WMU 438 constituents of the Cadomin census zone, which also exhibit the highest variability (SE=0.05, each) in lamb: ewe ratio and are respectively (df=23, t=-1.75, p=0.05) (df=22, t=-1.53, p= 0.07) approaching significantly greater values than the novel range in winter. The relatively high lamb: ewe ratio in WMU 437 compensates for the significantly lower ewes as a proportion of adults in WMU 437 than on other native ranges, elevating the proportion of lambs to the level found on other native range census zones. The high lamb: ewe ratio in WMU 438 results in the second highest proportion of lambs in the population when the proportion of ewes in the population is only the fifth highest. The novel range does not exhibit this relatively elevated lamb: ewe ratio in spite of being entirely encompassed by WMUs 437 and 438. The high productivity observed in WMUs 437 and 438 is consistent with WMU 436 which is also part of Cadomin, but not included in the preceding analysis because surveys were only conducted in winter 2011 and 2012. WMU 436 displayed high presence of ewes (76% and 81 % of adults in 2011 and 2012, respectively) and lambs (22% and 28% of the total population in 2011 and 2012, respectively). High lamb presence on native ranges adjacent to or proximate to L&GR suggests novel range is affected by additional mortality of lambs, or avoidance by ewes with lambs.

Bighorn sheep in WMU 446, within the Willmore, have also changed distribution to occupy novel range on a coal mine. Ewes in WMU 446, native range and novel range combined, comprised a high proportion of the adults in the 2009 and 2011 winter composition surveys, at respectively 74% and 78%. However, lambs as a proportion of the population were as low as that observed on L&GR in winter at 15% and 11% in 2009 and 2011 respectively. The proportion of lambs in WMU 446 is significantly less than that observed on the surrounding Willmore native range in 14 survey years from 1972–2011 in both 2009 ($n=14$, $t=5.59$, $p<0.01$) and 2011 ($n=14$, $t=8.8$, $p<0.01$). The lamb: ewe ratio of 0.24 in 2009 ($n=14$, $t=5.58$, $p<0.01$) and 0.18 in 2011 ($n=14$, $t=8.8$, $p<0.01$) is lower than observed on the surrounding Willmore native range in 14 survey years from 1972–2011.

Immigration

Asymmetry between increasing abundance (Fig. 2.3, Table 2.2) and low productivity on L&GR (Fig. 2.5b) establishes that bighorn sheep presence on L&GR is a function of immigration. Asymmetry between decreasing abundance (Fig. 2.3, Table 2.2) and high productivity on novel range (Fig. 2.5b) is consistent with emigration, and establishes native range as a source. Stable abundance and composition at the northern Rockies focal scale (Fig. 2.4) and productivity at the census zone scale (Fig.

2.5b.) establish that a stable–to– positive birth to death relationship exists on native range, but not on novel range (Fig. 2.6). Demographics refute claims of high productivity and recruitment on the novel ranges of L&GR and thereby provide conclusions that (1) productivity on novel range is not equal to or greater than native ranges, (2) ram and ewe presence on novel range is not an independent population and (3) recruitment from novel range does not support bighorn sheep abundance on native range census zones. Low productivity allows only for immigration to account for the large increased abundance on L&GR.

Increased bighorn sheep presence on L&GR novel range has been documented since 1982. Useful winter and pre-rut composition data is respectively available from 1982 and 1994–2011. Increases in ewe abundance (yearling ewes + ewes >1.0 years old), occurred in the pre-rut of three of the 18 years. If L&GR is a population independent of native range, the apparent ewe survival ($ewes>1.0\ yrs_{(n)}/\ ewes\geq 1.0\ yrs_{(n-1)}$) in each of the three years would be $\geq$ 110%. Additional information regarding (1) population dynamics and (2) seasonal distribution (Supplemental Table 1, Fig. 1, 2, 3, 4) corroborates immigration as the source of bighorns on the L&GR census zone.

Discussion

Population Vigour

A self-sustaining demographic population of bighorn sheep is expected if an occupied range is the source of the long-term late winter presence of ewes that are 60-70% of adults and lambs that are ~20% of total bighorn sheep (Fig. 2.6). Lamb: ewe ratios will typically be 0.35–0.45. Native range reproductive (adult sex ratio) and recruitment (lambs as a proportion of total bighorn sheep) resilience rendered the abundance of bighorn sheep in the northern Rockies resilient to environmental changes and population exploitation from 1982 to 2012, and arguably, as far back as 1972. At the finer spatial scale of the census zone, there is a relationship of high productivity and declining abundance on native range, and low productivity and increasing abundance of both sexes on the novel range of L&GR (Fig. 2.6). Low reproductive and recruitment potential distinguish L&GR from native range. Declines in rams on all native ranges and declines in ewes on native range most proximate to L&GR are consistent with expectations of greater population structure and more localized movement of ewes (Ball et al. 2007, Haanes et al. 2011), some independence of distribution between sexes (Ranta 1999, Singh et al. 2012) and distance mediated independence among females. If the decreasing ewe abundance in the combined Jasper-Cadomin-L&GR census zones is independent of increasing ewe abundance in the Clearwater, Nordegg and Willmore census zones, a sink effect may be occurring on L&GR. A corresponding local decline in rams is suggested by the persistence of the ram and ewe abundance and the adult sex ratio at the northern Rockies scale.

When distribution is ignored, estimating demographic parameters is problematic, affecting understandings of the value of habitat components, including identifying sources and sinks (Pulliam et al. 2011). Over the 30–40 year period examined in this study, bighorn sheep abundance and composition stability in the northern Rockies differs from study areas of relatively isolated populations and small range sizes which are typically characterized by variability in abundance, productivity and survival (e.g. Jorgenson et al. 1997, Jorgenson et al. 1998; Festa-Bianchet 1989, Festa-Bianchet et al. 2006). Multiple scales and greater area reveal the expected importance of distribution (emigration and immigration) and mating system (Ranta et al. 1999) in conjunction with birth and mortality dynamics. Bighorn sheep use space to benefit from and tolerate environmental variation.

Populations must be specifically identified and assessed because vital rates were found to vary in importance among bighorn sheep populations and to differ between small, declining or endangered populations and large, increasing or healthy populations (Johnson et al. 2010). Demographic (e.g. reproduction, recruitment and distribution effects on abundance and composition) and geographic patterns suggest probable scales, states and management hypothesis pertinent to conservation.

Reproductive and recruitment resilience identify safe operating spaces (*sensu* Rockstrom et al. 2009) to accommodate variability, uncertainty and surprise

Female skewed adult sex ratio is an adaptive advantage of bighorn sheep and presented here as the primary indicator of population vigour and measure of resilience to disturbance and change. Adult sex ratio represents the potential to contribute births, including fertility of rams and ewes, and is a measure of relatively long-term resiliency, capturing at least one generation of ewe recruitment and survival (estimated at nine years, Loison et al. 1999). A general cause of biased sex ratios may not be demonstrable because changing environmental circumstances may vary the mechanisms involved (see reviews by McCullough 1999, Berger and Gompper 1999, Hoffman and Genoways 2012, Blank and Yang 2013). Additionally, the variance and relative importance of specific vital rates can change spatio-temporally within and between populations (Morrison and Hik 2007, Harris et al. 2008, Johnson et al. 2010). Population resilience may be reduced when vital rate adaptions evolved in response to feedbacks are suppressed by external drivers, (e.g. attractive sinks or management actions that elevate the removal of females) (Holling 1973, 1986, Carpenter 2001, Biggs et al. 2012, Curtin and Parker 2014). As sex ratio regresses to parity the resilience of the population declines. Therefore the probability that a relatively small shock will cause significant change in the population increases. We argue that adult sex ratio aggregates and manifests vital rates resulting from feedbacks generated by ecosystem components, and influenced by external drivers.

Female skewed sex ratio may increase male fertility by increasing the proportion of males that may breed, and may increase reproductive fitness by successful males breeding with more females (Haridas et al. 2014). Reproductive capacity is highest when females dominate the reproductive cohort in polygynous systems (Ranta et al. 1999) but an excessive skew increases vulnerability to stochastic events (Hoffman and Genoways 2012). Extreme skew towards the more frequent sex may counter selection for increased adult survival (Haridas et al. 2014). Extinction risk is believed to increase with male skewed sex ratios in both polygynous and monogamous species (Haridas et al. 2014).

Ewes constitute ~65% of adult bighorn sheep on all native ranges, except for the pseudo sink in WMU 437. Ewes constituted 64.9, 64.0 and 64.7% of all adults in the three time periods (respectively 1982–83, 1986–88, and 2011) for which total abundance can be estimated for the entire northern Rockies study area. Relatively stable adult abundance at the scale of the northern Rockies and consistent late winter composition on native range (Fig. 2.6) suggests that a recruitment potential of lambs as ~20% of total bighorn sheep may be required for population persistence. The 20% lamb composition of total bighorn sheep is confirmed by aerial inventory of bighorn sheep throughout Alberta since 1972 (AEP data, Alberta Bighorn Sheep Management Team). Adult sex ratio (reproductive potential) can be viewed as the population's adaptive response to controls of environmental variation and evolution, incorporating time scales of one generation to centuries. Annual proportion of lambs (recruitment potential) is viewed as the response to controls of the adult sex ratio and current (immediate year and possibly a small number of preceding years) environmental and distribution conditions.

Female presence is of overall importance to population growth (Ranta et al. 1999). Adult sex ratio determines the recruitment potential of an accompanying lamb: ewe ratio. Ewes comprising 60-70% of adults are necessary to achieve ~20% lambs as a proportion of total bighorn sheep, even if a relatively high lamb: ewe ratio exists. Adult sex ratios of 65% or 50% ewes both with 0.4 lambs: ewe will respectively have 20.6% and 16.6% lambs as a proportion of total bighorn sheep. Elevating ewes to 65% from 50% of adults, while holding ram abundance constant, requires an 85% increase in ewes, demonstrating the importance of maintaining ewe composition. Ewe skewed sex ratio will (1) increase the potential to generate lambs and therefore the recruitment potential and (2) the fertility of rams

(Haridas et al. 2014). Where fertility depends on the adult sex ratio (frequency dependence) increasing ewe survival will increase the ratio of ewes to rams.

If population identity and survival are known (DeCesare et al. 2012) and independent population growth and size estimates are available (Harris et al. 2008) age ratios may detect severe population declines, monitor survival rates of young (Harris et al. 2008) and contribute to monitoring demography (DeCesare et al. 2012). These criteria cannot be met in the northern Rockies, or in most free ranging ungulate populations supported by dynamic ecosystems. Intensive research programs are required to meet these criteria. Further, ewe abundance increased in Clearwater and Nordegg in spite of low lamb: ewe ratios in 4 consecutive surveys from 2005 to 2011, and age ratios were not correlated with population growth in mountain goats (*Oreamnos* americanus) within the northern Rockies (Cote et al. 2001). Also, significant increases in abundance in L&GR occurred although the lamb: ewe ratio does not differ from native ranges except for being lower than the adjacent WMU 437.

Ram, ewe and lamb abundance on L&GR is highest in the fall, declining in the winter (Supplemental Fig. 3, 4) and lowest during summer (AEP unpublished data). Seasonal habitat selection demonstrates dependence on native range for energy and nutrient acquisition (summer) and conservation (winter). Late summer distribution of ewes to L&GR transfers lamb productivity from native range selected during the lambing and primary nutrient and energy acquisition period.

L&GR reproductive and recruitment resilience is not expected to sustain a population and establishes that bighorn sheep presence is dependent, possibly entirely, on immigration from native ranges. The winter presence on L&GR of ewes as proportion of adults and lambs as proportion of total bighorn sheep, of respectively 0.49 and 0.15 from 1994–2011, cannot support population maintenance for an extended time, and cannot support growth. Claims of an independent population and a rapid internally generated population increase are refuted by low reproductive and recruitment resilience throughout the period of rapid increase in abundance from 1982 to 2011 (from an estimated 43 to 941 animals in winter) and the resulting high density of bighorn sheep $\geq$1.0 yrs. old (939 and 794 respectively in fall and winter on a 41.9 km^2 mine disturbance limit (MDL)(Cristescu 2013). The balanced sex ratio on L&GR (versus skewed sex ratios on native range) is consistent with younger rams distributing with ewes and older rams distributing independent of ewes and over greater distances. Occupation by bighorn sheep of L&GR is consistent with the realized niche (area occupied by a population) typically being larger than the fundamental niche (area that provides resources supporting the population) (Pulliam 1988, Hull et al. 2011).

Emigration from high productivity native range is evidenced by the pattern of declines in rams on all five census zones and ewes on the two census zones (Fig. 2.4), closest in distance to the novel range (Fig. 2.6), supporting the evidence of immigration to novel range from native ranges. The consistency of abundance and composition, and reproductive and recruitment resilience, allow native range ecological resilience to maintain conditions that sustain bighorn sheep at the northern Rockies and census zone scales. The mosaic of habitat qualities may include sinks, not detectable with our data, which draw animals away from ideal sites, or temporarily accommodate animals that eventually disperse back to sources (citations in Murphy 2001).

Demographic populations can be approximated, and subsequently tested when genetic populations are identified. Demographic approximations should consist of at least 125 ewes (AEP Bighorn Sheep Management Group) that comprise 60 - 70%, centered on 65%, of the sampled adults (Fig. 2.6). Adult sex ratio is expected to test the suitability of a sample from a subject habitat to represent a population, and cause sampling of a bighorn sheep assemblage over a spatial scale that could support the aggregation on a subject habitat. For example, on all native ranges the desired adult sex ratio can be achieved at the spatial scale of the census zone or less. A demographic supporting the pseudo-sink in

WMU 437 is obtained by expanding the sample collection to include the Cadomin census zone. Of course this process does not mean that our census zones represent discrete demographic populations, which may occur at smaller spatial scales or include parts of two or more census zones and be further complicated by differences between ram and ewe population structure and movement (e.g. Ranta et al. 1999). Alternatively the aggregation on novel range of L&GR requires sampling at the spatial scale of the entire northern Rockies to define a sustainable demographic population.

Environmental Quality

We propose that adaptive capacity to achieve resilience is a consequence of broad scale connectivity among habitat variation, and further that adaptive capacity is diminished by the cumulative effects of small disturbances (Fig. 2.6). Small disturbances individually or in smaller groups are commonly not expected to be identifiable as significant (Scheffer et al. 2001). The persistence of bighorn sheep on specific range segments is expected to depend on distribution within an encompassing spatial extent that supports the demographic population. Connectivity resulting from distribution influences resilience by affecting both the spread of disturbance and the recovery from disturbance (Holling 1986, Biggs et al. 2012). Bighorn sheep movement among habitats involves complex interaction among topography, resources and differences between sexes (Ranta et al. 1999, DeCesare and Pletscher 2006, Hogg et al. 2006, Dibb et al. 2008). Ecosystem structure and function can be affected by changes in movement (Holling 1973, Lundberg and Moberg 2003, Singh et al. 2012). On native range the consistency of ewe skewed sex ratios and lambs as a proportion of total bighorn sheep suggests connectivity movements are broadly symmetrical. An expectation that a finer scale continuum of sources and sinks (Thomas and Kunin 1999) exists is demonstrated by the apparent pseudo-sink in WMU 437 (Fig. 2.6), where presence is sustained by internal productivity, and elevated by immigration that is greater by rams than ewes.

The capability to distribute among a mosaic of habitat qualities, that may be dynamic over time, enhances resilience by effects such as access to net benefit resource opportunities, minimizing exposure to predators and accommodating coexistence with other biota that constitute and contribute to self-sustaining ecosystems. However, human-induced ecological changes may influence the adaptive benefit of distribution, diminishing resilience that supports persistence of a large population. Shifts in surrounding areas can change the ecological resilience of high quality habitat areas (Groffman et al. 2006). Source-sink population structure is expected to emerge where asymmetrical dispersal occurs between two habitats at demographic equilibrium (Pulliam 1988, Holt 2011). Attractive sinks that diminish productivity are common consequences of ecological changes resulting from human uses of land and resources (Delibes et al. 2001; Donovan and Thompson 2001, Schlaepfer et al. 2002, Battin 2004, Sih 2013). Predation equilibria that bighorn sheep are believed to achieve over large temporal and spatial scales may be jeopardized by ecological changes, such as human-caused landscape fragmentation, that increase the frequency or intensity of elevations in predation that periodically occur on geographic constituents of bighorn sheep range (Festa-Bianchet et al. 2006).

Changes in bighorn sheep distribution in the northern Rockies, including occupation of L&GR, are emergent qualities generated by self-organization of a large population and a relatively pristine ecosystem responding to the shock from surface mining. Attracting bighorn sheep or other wildlife from source habitats on native ranges to habitat occurring on mined areas may function to spread the mining disturbance (Groffman et al. 2006). Ram and ewe bighorn sheep are affected by this shock over areas that may be respectively two and approaching three orders of magnitude greater than the 41.9 km^2 MDL. Greater variability in reproductive and/or recruitment resilience, resulting from declines in ewes occurring over a smaller area but at a greater magnitude than rams, position Jasper and WMU 438 closer to the threshold of an alternate state (Fig. 2.6). Ecological processes and conservation can be affected at a much larger scale than pertinent shock. As a result cumulative effects management, to be effective, is obliged to understand the scales influenced by disturbances.

Colonization of novel range may have reduced the ecological resilience of bighorn sheep across the northern Rockies. Stressors demonstrably affecting distribution and possibly affecting survival, particularly of lambs on novel range (Supplemental Table 1) may be challenging the structure, function and quality of the bighorn sheep population. Increased emigration from native range or altered historical distribution patterns because of holdover on novel range are consistent with declines in abundance on native ranges. The persistence of the ewe skewed adult sex ratio on all native range census zones, and apparent connectivity by bighorn sheep movement among census zones, may constitute resilient properties that manifest less apparent adaptive capacities or processes.

Magnitude of asymmetry between productivity and either numerical response or attractiveness (high density presence) on L&GR are consistent with a sink constituting an ecological trap (Donovan and Thompson 2001, Battin 2004). Low inter-annual variation of pre-rut composition (Fig. 2.6) is consistent with a high resilience that perpetuates ongoing attraction to low productivity novel range. Greater variability in winter composition of bighorn sheep on L&GR (Fig. 2.6) is consistent with lower resilience and more potential for a management-induced change to a state that diminishes distribution to novel range. Grizzly bear (*Ursus arctos)* response to the same novel range, characterized by dependency on the surrounding native ecological communities and residual native vegetation within the novel range, diet shifting to planted agronomic vegetation, perceived increased mortality risk and no identified population or individual animal benefit (Cristescu 2013), are consistent with bighorn sheep response.

Redundancies and complexity allow ecological systems to respond to varying types and magnitudes of stress (Holling 1986; Biggs et al. 2012; Walker and Salt 2012). Simplifying ecological systems (e.g. simplified terrain features or vegetation communities, suppression of predators or primary prey) to enhance productivity of one species or facilitate exploitation of a resource, is fraught with emergence of unanticipated issues, which is a characteristic of the self-organizing systems that societies are trying to perpetuate and benefit from (Holling 1986; Salt and Walker 2012). Maintaining system complexity and redundancies (Biggs et al. 2012) are essential to accommodating the surprises that are inevitable (Lindenmayer et al. 2010) and to maintain potentials to exploit land and resources.

Distribution that causes seasonal high concentrations of bighorn sheep may pose risks to northern Rockies populations by the spread of disease, potentially reducing the high productivity and therefore resilience of native ranges. Diseases are among the agents responsible for severe declines in wild sheep populations in the southern regions of North America. When introduced to a population, diseases (e.g. pneumonia) may persist and pose risk for many years (Cassirer and Sinclair 2006; Cahn et al. 2011; Besser et al. 2012). Attraction of bighorn sheep to high concentration ranges such as L&GR, and movement of these animals to proximate native ranges that are closely connected to more distant native ranges, provides a source and wick to transmit contagious disease throughout the Northern Rockies.

Acknowledging that the current process of mining and reclamation will result in a change of state allows for focus on development of a state compatible with proximate native range, an essential achievement if the benefits of natural systems are to be maintained along with human use. Alternatively, if restoring a compatible ecosystem fails, this change of state may be managed for by isolating the mining residual from proximate lands. The use of fencing for large-scale exclusion of wildlife has proven effective (e.g. Trans-Canada Highway in Banff, Dingo (*Canis dingo)* fence in Australia) and relocation of ewes, lambs and young rams to native ranges in Jasper is consistent with historical and current translocation programs for wildlife including bighorn sheep. Relocation of young rams to

Nordegg and Clearwater, following confirmation that Cadomin, Clearwater and Nordegg are the same genetic population for rams, would be consistent with the decline in ram abundance on these ranges.

Surprises

Learning from surprises will remain among the most instructive of scientific and management actions, particularly as environmental variability increases. The large and contiguous bighorn sheep range and population in the northern Rockies enabled ram movement at distance and magnitude that will surprise those orientated to local or small, somewhat isolated ranges. Stable-to-increasing ewe abundance and persistent low lamb productivity in Clearwater and Nordegg from 2005–2011 suggests that some distributional influence has compensated for low productivity in those years, contrary to the assumption that bighorn sheep are relatively sedentary on restricted ranges. The range shift of ewes from Jasper is coincident with sustained productivity, but not accompanied by a compensatory recruitment to sustain abundance in Jasper. Surprisingly complex continuing relationships between this source habitat and a consumer habitat may exist. The determination of a pseudo-sink in WMU 437 is a surprisingly different than the self-sustaining population currently assumed to exist, and consistent with greater movement particularly by rams than previously perceived. High population vigour and very limited human harvest (an external driver) of ewes in Willmore is contrary to a management dogma, but consistent with synergistic relationships between herbivores and plants and predators and prey, and vital rate variation in response to environmental variation. The relatively low population reproductive vigour of the high density bighorn sheep aggregation occupying novel range on L&GR is consistent with ecological science, but contradicts some explanations of convenience. Environmental variation and human induced external drivers are expected to continue to influence feedbacks between populations (fast variables) and environmental controllers (slow variables) that affect habitat quality.

Conclusions

Management intended to sustain wildlife populations needs to link demographics and distribution with environmental components and prioritize improving or maintaining environmental quality. Habitat quality can be categorized by assessing the value of occupancy from reproductive resilience, recruitment resilience and changes in abundance. These are practical surrogates for large spatial scale (focal, census zone) interactions of birth, death, immigration and emigration, the only ways that individuals move into or out of populations. Demography is essential to understanding the state of a population and can define distribution. Safe operating space is identified for adult sex ratio (~65% ewes) and lamb composition (~20% of total bighorn sheep abundance). Relatively high and annually consistent reproductive and recruitment potentials on native range are expected to contribute to a resilience that supports persistence of a vigorous bighorn sheep population, including by providing a source of animals to disperse to pseudo or true sinks and by limiting the magnitude and therefore the associated risks of skewed age structure.

Sustaining high productivity native range needs to remain a conservation priority, but also must recognize that meaningful enhancement of native range may not be feasible or required. Processes and properties associated with the (1) internal ecosystem components of slow variables and feedbacks, (2) connectivity and (3) diversity and redundancy have been proposed as principles for enhancing resilience (Biggs et al. 2012) and are therefore essential management and research priorities. External drivers, implemented by management programs or resulting from radical environmental change, that override or substitute for internal environmental components pose a threat to ecosystems composed of co-evolved components. The conservation priority of distribution needs to be managed to maintain the genetic and ecological benefits of bighorn sheep movement among native ranges but render insignificant the dispersal to novel range sinks. Essential to maintaining public benefit, including continued resource exploitation and ecological services, may include overcoming the resilience of anthropogenic sinks.

Fig. 2.1. Resilient Bighorn Sheep Study Area Map – West Central Alberta and part of Northeastern British Columbia

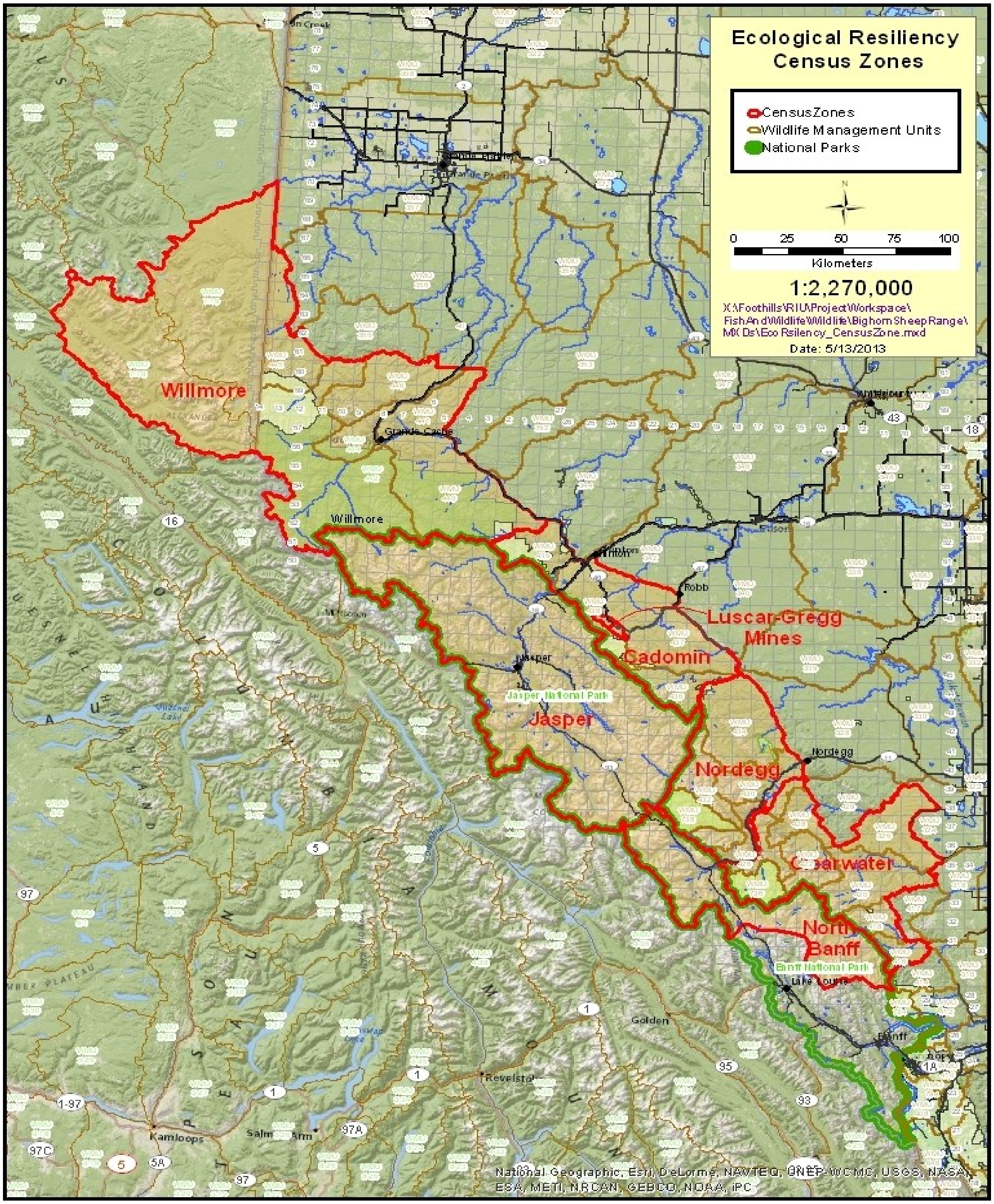


Fig. 2.2. Changes in the abundance of ram and ewe bighorn sheep at the scale of the entire Northern Rockies study area from 1982–2011, at 3 years when data is available for the entire study area. Ewes are 64.9, 64.0 and 64.7% of adults, respectively in 1982-83, 1987-88, and 2011.

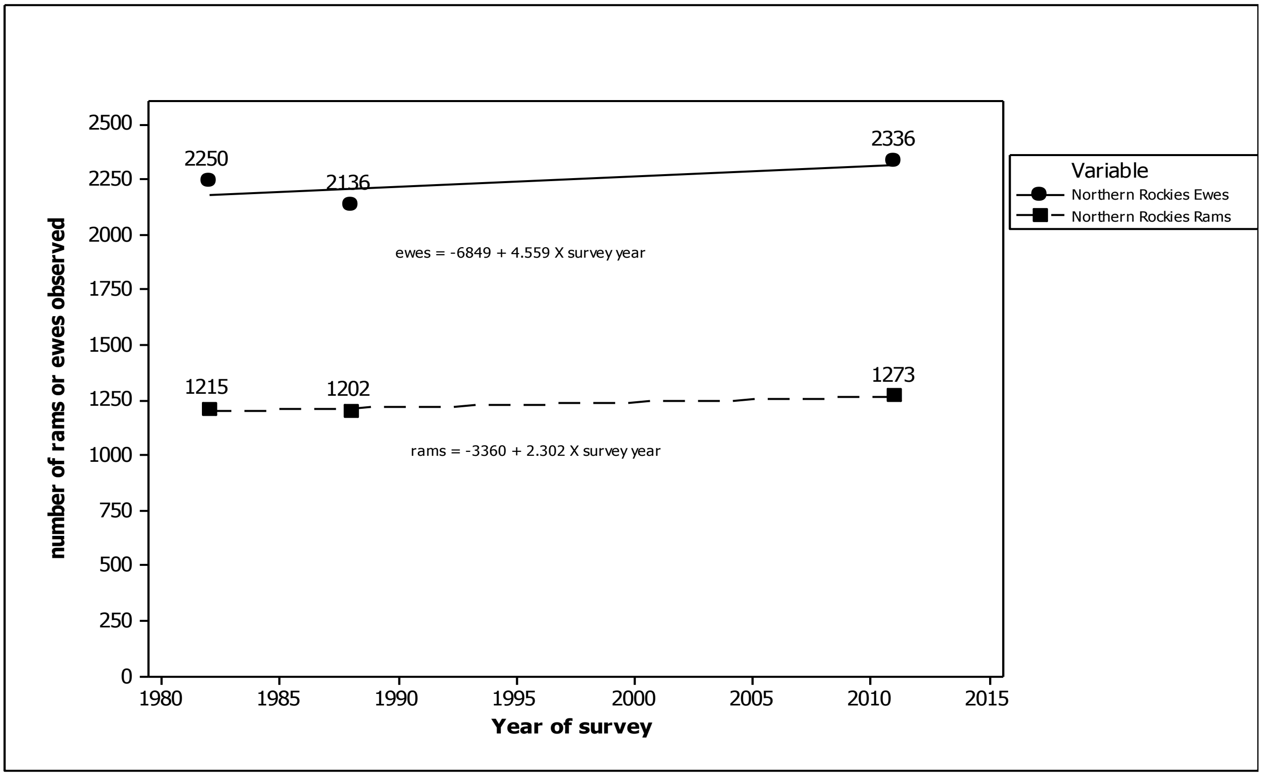


Table 2.1. Significance of changes in rams and ewes depicted in Fig. 2, total adult abundance, and ewes as a proportion of adults at three years at the northern Rockies scale.

Demographic	Chi-sq.	DF	p-value
Ewes	3.321	2	0.190
Rams	0.836	2	0.658
Total Adults	0.011	2	0.994
% Ewes	2.799	2	0.247

Fig. 2.3. Changes to ram and ewe bighorn sheep abundance in six census zones in the Northern Rockies from 1982–2012. Decline in rams on all five native range census zones and decline in ewes on Jasper and Cadomin equals the increase in rams and ewes on L&GR census zone.
*significance @0.05, ** significance @0.07; see Table 2 for p-values of each census zone

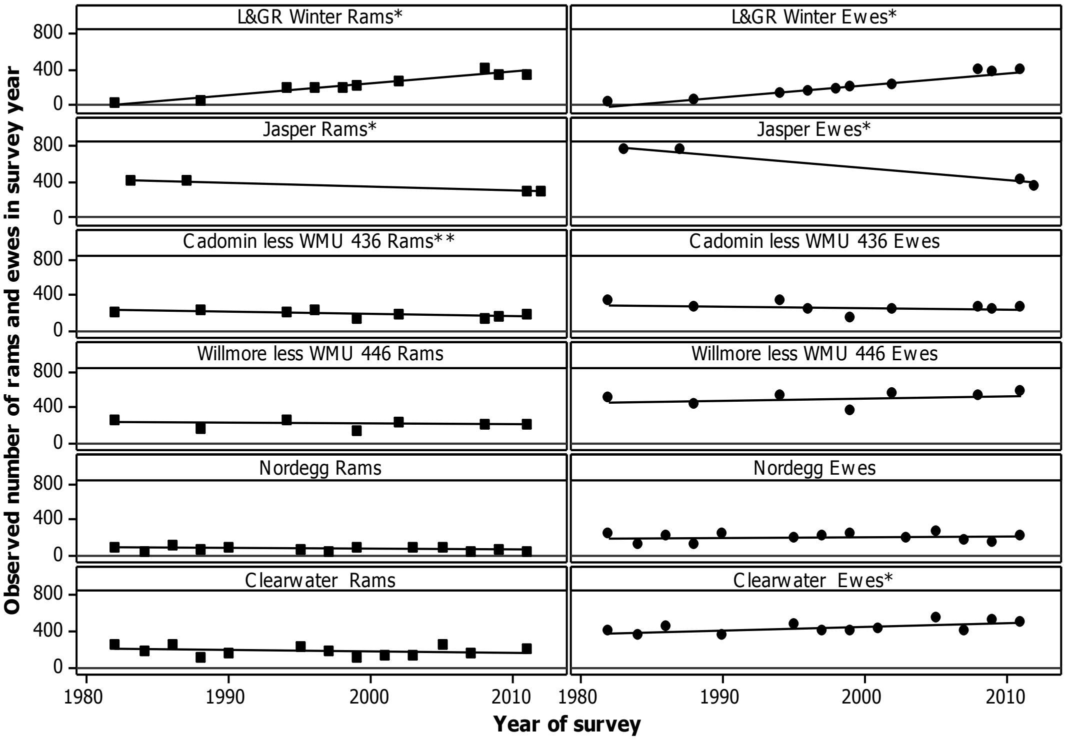


Table 2. 2. Trends in ram and ewe abundance in six census zones for three time periods. Asymmetry in decline in rams and increase in ewes on the three native range census zones (Clearwater, Nordegg, Willmore) most distant from L&GR. Decline in both rams and ewes on two native range census zones (Cadomin and Jasper) closest to L&GR. Disagreements in trend between 1972—2012 and 1982—2012 and agreement between 1980—2012 and 1982—2012 for both sexes indicates that 1972—1980 was a period of learning how to survey bighorn sheep and does not measure growth.

Jasper time periods are 1967–2012 and 1982–2012

Table 2.2a. Trends in ram abundance in six census zones for three time periods

Census Zones	1972 - 2012				1980 - 2012				1982 - 2012			
	Trend	**df**	**t**	**p**	**Trend**	**df**	**t**	**p**	**Trend**	**df**	**t**	**p**
Clearwater	increase	17	0.51	0.618	decrease	13	-1.01	0.330	decrease	12	-0.67	0.519
Nordegg	increase	14	0.33	0.743	decrease	12	-0.70	0.498	decrease	12	-0.70	0.501
Jasper	decrease	4	-0.53	0.632	n/a	n/a	n/a	n/a	decrease	3	-10.8	0.008
Cadomin less WMU 436	increase	12	0.60	0.503	decrease	9	-1.41	0.197	decrease	8	-2.14	0.070
Willmore less WMU 446	increase	11	0.79	0.447	decrease	7	-0.18	0.864	decrease	6	-0.47	0.657
L&GR	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	increase	9	11.97	<0.001

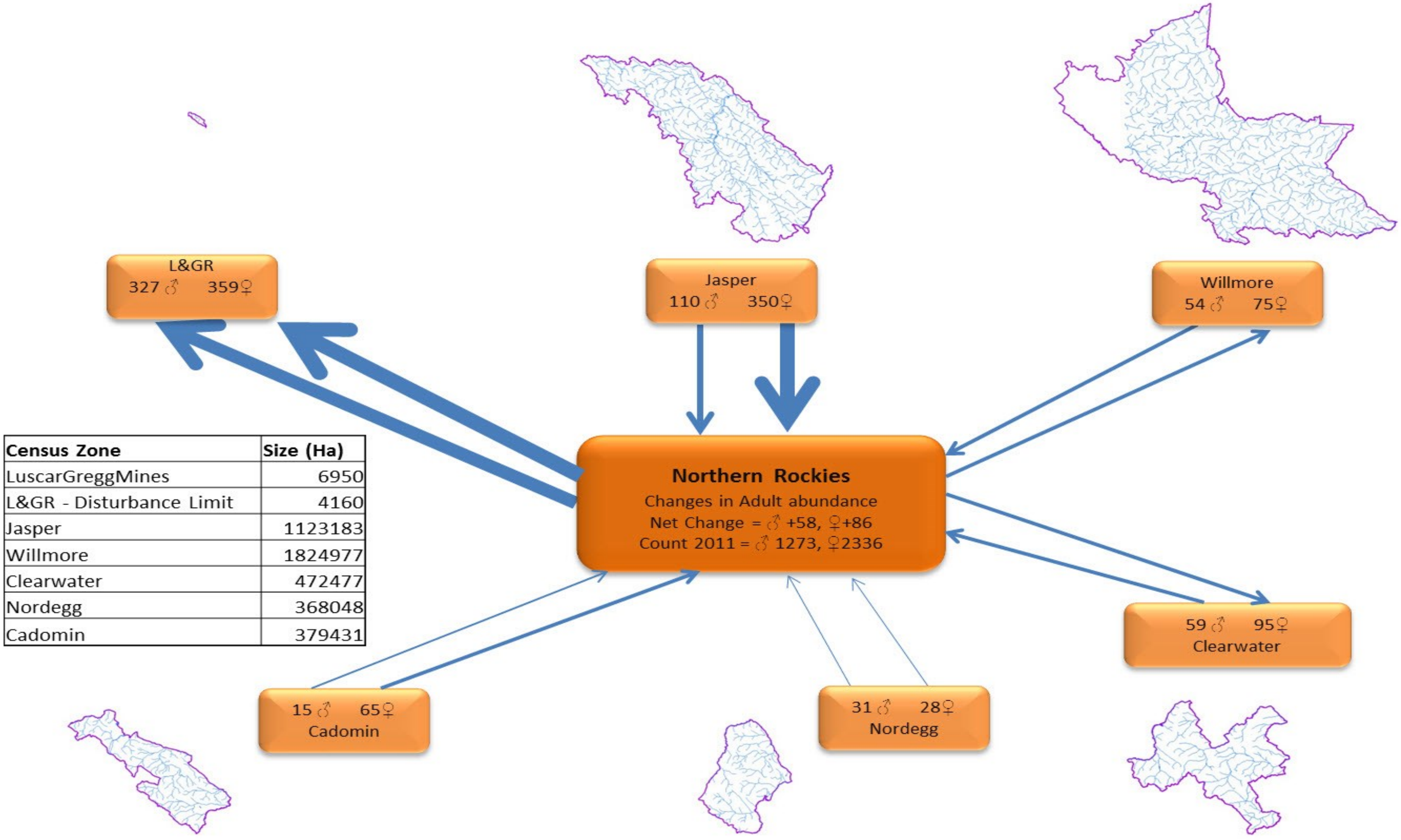
Table 2.2b. Trends in ewe abundance in six census zones for three time periods

Census Zones	1972 - 2012				1980 - 2012				1982 - 2012			
	Trend	**df**	**t**	**p**	**Trend**	**df**	**t**	**p**	**Trend**	**df**	**t**	**p**
Clearwater	increase	14	4.12	0.001	increase	12	3.07	0.011	increase	11	2.35	0.040
Nordegg	increase	14	1.83	0.091	increase	12	0.29	0.779	increase	12	0.34	0.742
Jasper	decrease	4	-2.20	0.115	n/a	n/a	n/a	n/a	decrease	3	-9.43	0.011
Cadomin less WMU 436	increase	12	0.85	0.414	decrease	9	-0.75	0.474	decrease	8	-1.16	0.286
Willmore less WMU 446	increase	10	2.44	0.232	increase	7	0.75	0.484	increase	6	0.86	0.423
L&GR	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	increase	9	12.44	<0.001

Table 2.3. Annual rates of Increase for two time periods, 1978–1980 and 1972–1980 for four census zones, establishing that 1972–1978 was a period of learning how to conduct bighorn sheep aerial surveys.

Census Zone	**1978-1980**				**1972-1980**			
	Rams		**Ewes**		**Rams**		**Ewes**	
	1980/1978	ƛ	1980/1978	ƛ	1980/1978	ƛ	1980/1978	ƛ
Clearwater	237/196	1.105	328/304	1.040	237/113	1.102	328/351	0.992
Nordegg	82/74	1.054	235/71	2.270	82/32	1.133	235/104	1.133
Cadomin less WMU 436	153/154	1.000	211/95	1.634	153/97	1.060	211/209	1.008
Willmore less WMU 446	191/146	1.155	499/320	1.283	191/108	1.077	499/360	1.043

237/196 = # of rams observed in 1980/ number of rams observed in 1978
328/304 = # of ewes observed in 1980/number of ewes observed in 1978



Census Zone	Size (Ha)
LuscarGreggMines	6950
L&GR - Disturbance Limit	4160
Jasper	1123183
Willmore	1824977
Clearwater	472477
Nordegg	368048
Cadomin	379431

Fig. 2.4. Changes in Winter Abundance of Adult Bighorn Sheep Among Six Census Zones in the Northern Rockies from 1982–2011

Fig. 2.5a. Best proportion of ewes among adults in a bighorn sheep aggregation allows for greater presence of lambs and ram fertility

Best proportions: ▬ lambs as % of total sheep (~0.20) ▬ ewes as % of adult sheep (~0.65)

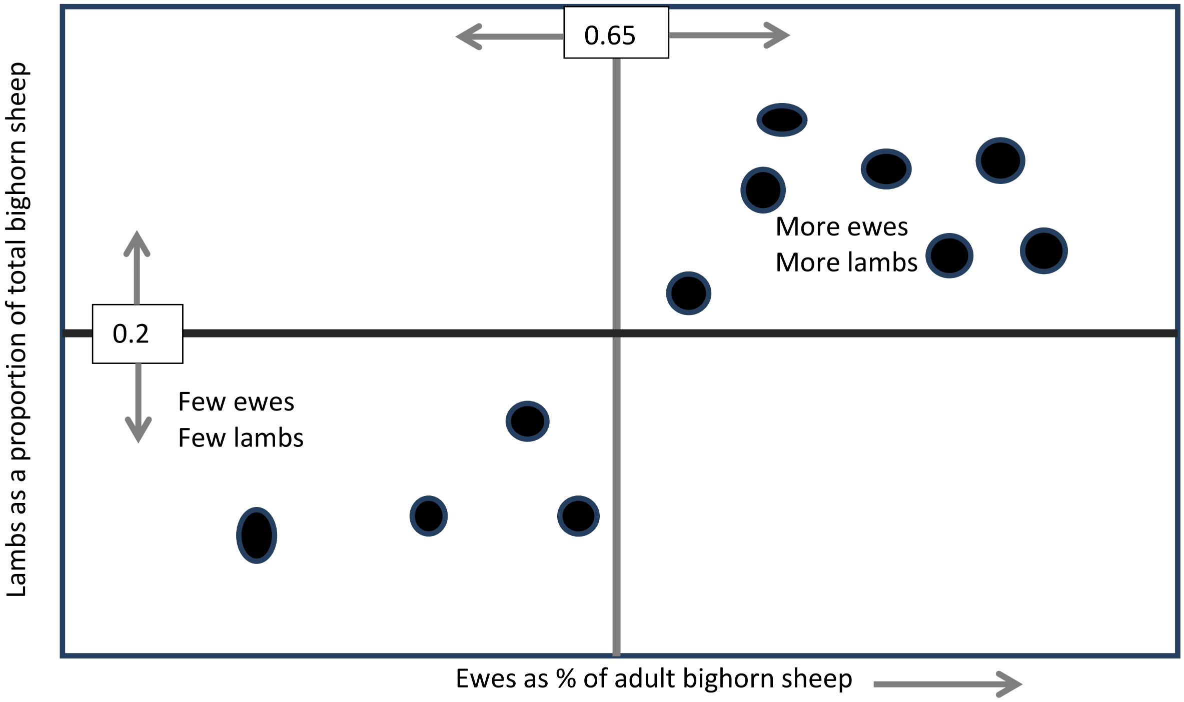
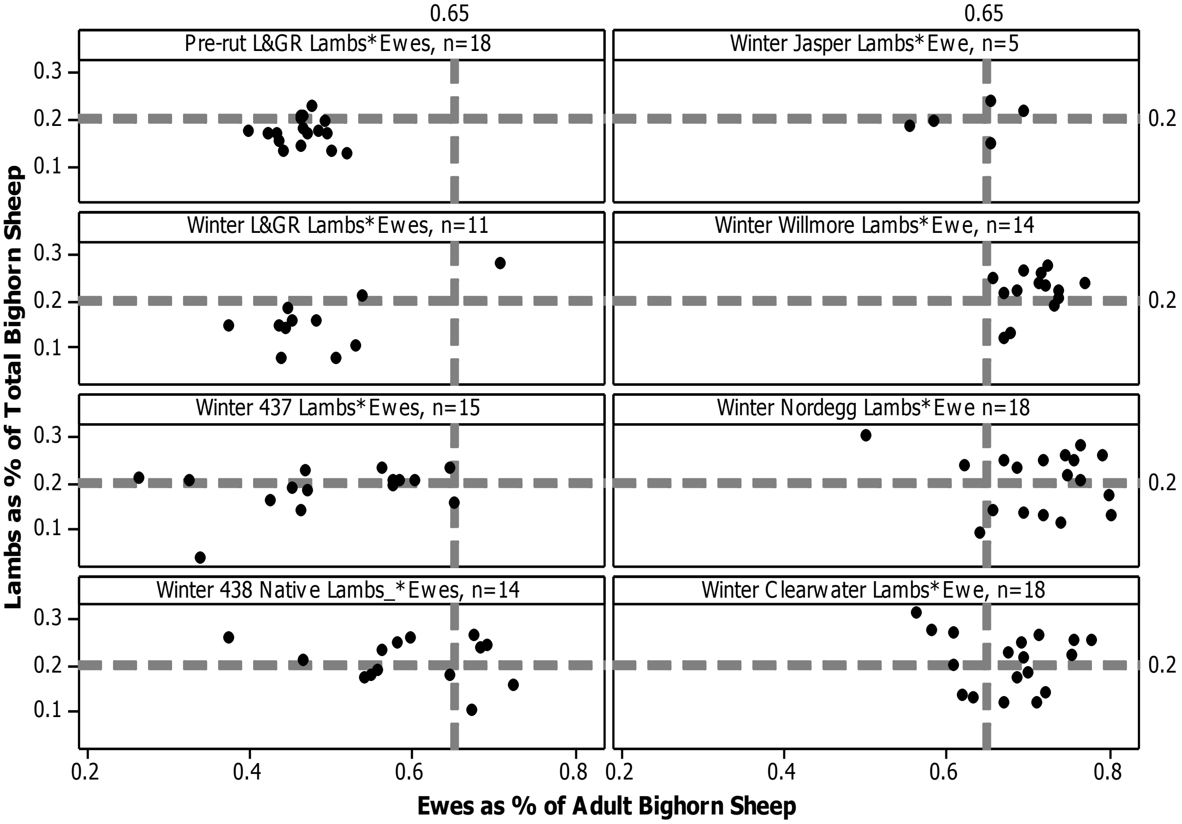


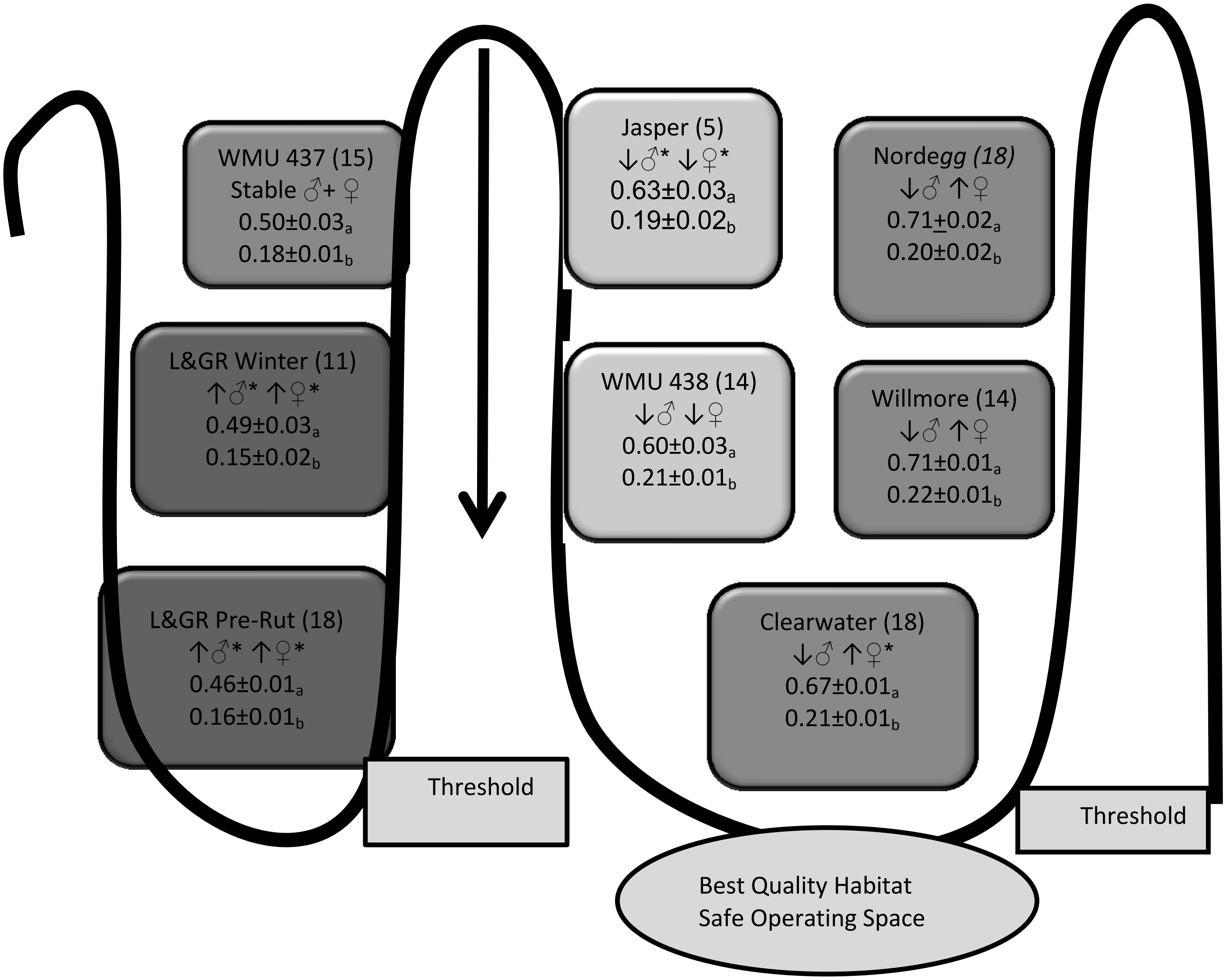
Fig. 2.5b. Reproductive (ewes as % of adults) and recruitment (lambs as % of total bighorn sheep) resilience in winter on census zones in the Northern Rockies. Census zones are tested for the presence of ~65% ewes as proportion of adults and ~20% lambs as proportion of total bighorn sheep. Cadomin census zone is divided into WMUs 437 and 438, which encompass L&GR. L&GR census zone is tested both in the pre-rut and the winter. Native range has high reproductive and recruitment resilience. Surveys of census zones are from 1972—2011, except Jasper which is 1967—2012. n=#of surveys.



Ewes as % of adult bighorn sheep one-way ANOVA: $F_{7,105} = 28.1$, $r^2 = 65.2\%$, $p<0.001$
Lambs as % of total bighorn sheep one-way ANOVA: $F_{7,105} = 2.73$, $r^2 =15.4\%$, $p=0.012$

Fig. 2.6. Safe Operating space for Population States and Potential Resilience of Bighorn Sheep Census Zones in the Northern Rockies 1982–2012 **(Mean ± SE)**
Composition 1972-2012, (n) = # of surveys; * = significant change in abundance 1982 – 2012

Environmental quality on native range (fundamental niche) fosters ecological resilience, measured by adult sex ratio (a) and proportion of lambs (b), that by distribution sustains bighorn sheep in the northern Rockies, including supporting the native pseudo-sink of WMU 437 and by immigration the presence on the attractive sink on the novel range of L&GR (expansion of realized niche) . Resilience of the attractive sink is eroding native range resilience shifting native range populations towards the upper and lower thresholds of the safe operating space of the desired state.



Chapter 3

Selenium Bioavailability to Ungulates in Western North America: Hormesis as a Form of Ecological Resilience

Introduction

Variation in trace mineral bioavailability among habitats often has subtle, difficult to detect and unpredictable effects on ungulate population fitness (Flueck et al. 2012). This complexity of bioavailability and effect is exemplified by selenium, a micronutrient that is a hormetic, essential to life, but with adverse effects resulting from both deficient and excessive dietary intake (Quinn et al. 2011, Barillas et al. 2011, Flueck et al. 2012). Ungulates acquire selenium relative to the bioavailability in their habitat and both selenium deficiency and toxicity are problems worldwide (Barillas et al. 2011; Flueck et al. 2012). Mountain and human altered environments are respectively prone to selenium deficiency or toxicity (Hebert and McTaggart- Cowan 1971, Terry et al. 2000, Quinn et al. 2011, Flueck et al. 2012, Poppenga et al. 2012, Hladun et al. 2013). Human activities are associated with both increases and decreases in selenium bioavailability (Hladun et al. 2011, Flueck et al. 2012, Eiche 2015) which lead to novel or chronic problems for ungulate populations. Determining a safe operating space (*sensu* Rockstrom et al. 2009) may provide a conceptual framework to accommodate ecological dynamism, uncertainty and variability of selenium bioavailability.

Resilience theory provides concepts and perspectives to assess the quality of complex ecological systems subject to uncertainty and emergent properties (Holling 1986, Walker and Salt 2012, Curtin and Parker 2014). Ecological resilience is concerned with maintaining the existence of function by focusing on persistence, change and unpredictability (Holling 1996). Excessive reductionism and focus on proximate factors obscures characteristic variability, ultimate causes of variation, existence and value of surprises, and accommodation of uncertainty (Holling 1973, Holling 1986, Doak et al. 2008, Contamin et al. 2009, Lindenmayer et al. 2010, Curtin and Parker 2014). Our interest here is to identify selenium bioavailability that indicates geochemical or herbivory processes that challenge habitat quality.

Effects of deficient or toxic selenium bioavailability are believed to be largely subclinical (Hebert and McTaggart-Cowan 1971, Flueck et al. 2012). These effects manifest in mammals as poor population performance, principally reduced reproductive success and recruitment, without apparent cause or where proximate factors may obscure primary factors (Hnilicka et al. 2004, Flueck et al. 2012). Overt expressions of deficiency or toxicity are expected to occur only after stress (Robbins et al. 1985). Only pronounced selenium deficiency or toxicity is lethal independent of other stress factors (Rucker et al. 2008, Rederstorff et al. 2006, Quinn et al. 2011, Flueck et al. 2012).

The interval between selenium deficiency and toxicity is therefore important to management of wildlife habitats in Western North America. The interval of adequate and safe selenium availability has not been documented for wild ungulates (Poppenga et al. 2012), but is known to be relatively narrow in mammals (Terry et al. 2000, Trumble and Sorensen 2008, Quinn et al. 2011), within just one order of magnitude (Eiche 2015). The risk of exposure to selenium related stress and effects can be assessed from selenium presence in the blood of specific mammal populations (Underwood and Suttel 1999, Herdt & Hoff 2011, Poppenga et al. 2012).

Selenium deficiency or toxicity can affect structures such as hair, hoofs, horns and bones, alter physiological functions and cause biochemical defects (Pond et al. 2005). A selenium containing amino acid essential to all mammals is part of a selenoprotein series involved in a range of biochemical and physiologic functions, including affecting structural features, immune function and genetic coding (see Flueck et al. 2012 for a review). However, the most important function of selenproteins is thought to be as an antioxidant; scavenging the toxic products of aerobic respiration, hydrogen peroxides and oxygen containing free radicals (Shchedrina et al. 2010). The long-term recognition (Terry et al. 2000, Flueck et al. 2012) and well–established toxic effects of selenium have led to regulations and efforts to remediate, including phytoremediation of contaminated sites (Hladun et al. 2013).

Selenium bioavailability considered appropriate for domestic animals cannot be assumed appropriate for wild ungulates (Robbins et al. 1985, Hnilicka et al. 2004, McKinney et al. 2006, Poppenga et al. 2012). Some authors have speculated that wild animals may have evolved mechanisms to compensate for low bioavailability of selenium (Robbins et al. 1985, Samson et al. 1989), including endogenous (e.g. biochemical, physiologic) or stress-reducing behaviours. However, significant compensatory abilities have not been documented. Additionally, environmental quality may mediate the consequences (Walker and Salt 2012) of relatively high or low selenium bioavailability on population vigour.

Ungulates acquire selenium from the environment through plants. Selenium taken up by a plant is a function of the form of selenium in the soil (e.g. Flueck et al. 2012, Barillas et al. 2012, Elche 2015). Selenite and selenate, the bioavailable selenium species (elemental Se and selenide species are bio-unavailable), are taken up by plants inadvertently as part of the process to acquire the essential element sulphur (Flueck et al. 2012) and assimilated to organic selenium compounds (Terry et al. 2000). Selenium is differentially stored among plant parts and among plant species (Fordyce et al. 2000, Terry et al. 2000, Barillas et al. 2012). Selenium distribution varies across the landscape and with soil chemistry (Fordyce et al. 2000, Flueck et al. 2012), varying in soil over very small distances (e.g. within tens of micrometers) (Eiche 2015), and frequently at levels inadequate for terrestrial herbivores (e.g. Flueck et al. 2012).

Bioavailable selenium may be declining globally due to human activities (Fleuck et al. 2012). Fossil fuel combustion has increased atmospheric sulphur content, reducing selenium uptake by plants and diluting selenium availability. Additionally, acidification of the environment may also increase the presence of heavy metals and selenium sequestration or reduce selenium to biologically unavailable forms. Wildlife such as bighorn sheep (*Ovis canadensis*) that feed on naturally low selenium availability alpine habitats in the summer may transfer selenium to lower elevation winter ranges through winter and early spring related mortality. Lastly, plants cannot generally uptake forms of selenium excreted by animals (see Flueck et al. 2012).

Elevation of selenium bioavailability, including toxic concentrations, are also attributed to human activities such as mining, particularly coal mining, irrigation and fossil fuel combustion (Sasmaz 2009, Hladun et al. 2013, Eiche 2015) and have long been recognized (Flueck et al. 2012), described (Terry et al. 2000) and costs estimated (Lemly and Skorupa 2012). Addressing the risks and costs associated with industrial elevated selenium has been largely unsuccessful (see Lemly and Skorupa 2012). Examples of unresolved selenium contamination in the Rocky Mountains include coal mines in west-central Alberta and southeastern British Columbia.

Mountain ranges such as the Rocky Mountains have low concentrations of naturally occurring selenium. This circumstance has been suggested as a contributing cause of the long-term decline in bighorn sheep in the United States (Hein et al. 1994, Hnilicka et al. 2004, Poppenga et al. 2012). Low selenium bioavailability has been associated with lack of recruitment in California mule deer (*Odocoileus hemionus*) (Flueck et al. 1994). Bighorn sheep ranges in the northern Rocky Mountains of Alberta and British Columbia are relatively intact and have not suffered the same declines and fragmentation as populations in the United States, and to a lesser extent southern Canada. This intactness may allow for a higher quality environment providing ungulate populations with options to counter the stress of selenium deficiency or toxicity that are not afforded by compromised habitats in more developed landscapes.

We examine selenium levels in ungulates from western North America reported in the literature and from populations of ungulate species sampled in Alberta. We identified asymmetries in these patterns and estimated a safe operating space (*sensu* Rockstrom et al. 2009) for selenium in the environment. Managing for ecological resilience may provide the best opportunity to avoid approaching undesirable thresholds. We also discuss options that may increase the resilience of ungulate populations to naturally low or deficient selenium bioavailability and to human introduced risks of selenium toxicity.

Methods

We consider a population to be members of a species assemblage associated with a geographic space. This definition does not purposefully define a demographic or genetic population unit. Populations that have not been knowingly provided with enhanced dietary selenium sources are categorized as unsupplemented. Populations occupying known high selenium environments (i.e. surface coal mines) or purposely provided with and known to consume additional dietary sources of selenium were categorized as supplemented. It is possible that some populations categorized as unsupplemented are obtaining selenium supplementation from agricultural sources (i.e. salt blocks, irrigation), but that this uptake is not causing selenium levels that are greater than characteristically observed in ungulates. This circumstance, if it is occurring, would further serve to highlight the extremely high levels of selenium bioavailability that populations categorized as supplemented in this study are exposed to.

Selenium presence was determined from whole blood collected from 85 ungulate populations of seven species including two caribou ecotypes in western North America. Whole blood reflects both the erythrocyte and serum selenium pools (Herdt and Hoff 2011, Poppenga et al. 2012) and a wide range in selenium intakes, such as differential uptake on different days or locations on a range (Underwood and Suttel 1999). Blood selenium values continue to increase while enzyme and hair values plateau when selenium intakes are sufficiently high to pose risk of toxicity (Underwood and Suttel 1999). The greater availability of published reports based on selenium in whole blood relative to tissue or hair samples reflect the preference for the use of whole blood, and provide a broader and larger comparable sample. Reliable relationships between whole blood and tissues (e.g. liver or kidney) and hair have not been established (but see Flueck et al. 2012).

Selenium levels in whole blood of ungulates from western North America were compiled from the literature and original research. The literature provided data for 57 populations of six species (Robbins et al. 1985, Fielder 1986, Jessup 1990, Deirenfield and Jessup 1900, Oliver et al. 1990a, Oliver et al. 1990b, Flueck 1991, Flueck 1994, Hein et al. 1994, Heffelfinger et al. 1995, Dunbar et al. 1999, O'Hara et al. 2001, Stephenson et al. 2001, Hnilicka et al. 2004, Zager et al. 2005, Barber-Meyer et al. 2007), including for five populations (two captive) of two species from within Alberta (Samson et al. 1989). The effects of selenium supplementation were reported for two free ranging populations of mule deer (Flueck 1994) and one captive population each of moose (*Alces alces*)(Stephenson et al. (2001) and mountain goat (*Oreamnus americanus*) (Robbins et al. 1985).

In Alberta, selenium levels were determined from whole blood from a further 20 populations of four ungulate species, including resampling two free–ranging populations reported in Samson et al. (1989). Capture of animals and extraction of blood in Alberta was conducted in compliance with standards and protocols of the Alberta Wildlife Animal Care Committee, under authorities granted to wildlife biologists in the employ of Alberta Environment and Parks or predecessors. Aerial net gunning was used to capture 69 animals in three elk (*Cervus canadensis*) populations and 123 caribou (*Rangifer tarandus caribou*) in respectively four and five mountain and boreal ecotype populations. Two caribou populations were each sampled over two and three consecutive years. Fifty four bighorn sheep from four unsupplemented populations and 24 animals from one supplemented population were ground captured. Two hundred bighorn sheep were captured by drop net over six capture years (1999-2001 and 2012–2014) from one supplemented population. Ten mountain goats from one population were captured by box trap. Additionally, bighorn sheep from one Alberta population occupying a selenium supplemented–range were relocated to a range in Nevada and resampled 11 months later. This Nevada source is considered a separate population.

All Alberta ungulates were sampled with whole blood collected by jugular venipuncture with a sterile syringe, and quick-frozen in a vacutainer containing a sodium heparin fixative. Blood was kept frozen until analyzed. Trace mineral analysis was conducted by the Holmes Research Center at the University of Idaho utilizing standardized vapor generation ICP technique (U of Idaho 1997) including calibration replicates, with the exception of 10 caribou samples from two populations collected in January 2001.These latter samples were analyzed at the Alberta Research Centre, using the standard ICP analytical techniques for wet weight analysis (Feng 2002) as used at the Holmes Research Center.

Additional data was assembled from nine bighorn sheep ranges sampled in the Hells Canyon stretch of the Snake River in Idaho, Oregon and Washington (Idaho Fish and Game unpubl.Hells Canyon Initiative 2010). This included one population provided with selenium supplementation that was sampled both before and during a two month cessation of supplementation. These samples were also analyzed by standardized vapor generation ICP technique (U of Idaho 1997) at the Holmes Research Center.

Statistical analysis was conducted using Minitab© version 16. Normal distribution of the set of 85 population means and the occurrence of each mean within the 95% CI were assessed by the Anderson-Darling test, to strongly test the tails of the distribution. Largest extreme value was determined to be the best fit of the distribution. Variability in selenium levels among ungulate species was tested by Analysis of Variance. Linear regression of population mean selenium and the standard error of the means described the pattern of variability relative to the population mean. Results were corroborated by regression of the fitted value of the standard error to the residual of the fitted standard error. The projected distribution of selenium presence in individual animals in Alberta was plotted relative to the estimated safe interval for selenium in whole blood of ungulates. Projected distribution is based on 256 animals sampled from 17 populations of four species not associated with coal mines, and on the 224 animals sampled from two bighorn populations occupying coal mines.

Results

The 85 ungulate populations sampled were normally distributed within the 95% confidence interval, except the three largest extreme values (n= 85, AD = 0.323, p>0.250) (Fig. 3.1). Two of these three populations are associated with high selenium environments on coal mines in Alberta and the third with a purposely selenium supplemented population in Oregon. Selenium levels in unsupplemented populations did not exceed 0.30 ug/g, ranging from 0.015–0.286 ug/g (Fig. 3.1).

The unsupplemented population with the highest selenium levels, boreal caribou from the Chinchaga population (n = 21), had significantly lower selenium levels than the lowest supplemented population which was bighorn sheep from the Smoky River Coal Mine (SRC)(n = 24) (df = 31, t = - 3.14, p < 0.001). Selenium levels in unsupplemented populations were not different from the mean measured in the population with the next lowest selenium levels, except for the lowest four populations (Fig. 3.1), where selenium levels decreased in the population with the next lowest selenium level. Populations with the fourth and third lowest selenium levels, respectively the Shasta County California mule deer (n = 42) and Alberta's Ram Mountain bighorn sheep (n=72), were both represented by large sample sizes (df = 44, t = 15.86, p <0.01). The sample sizes for the lowest two populations were low at four and two animals respectively, which may have hindered the statistical analysis, but was not expected to significantly influence the ordination of selenium levels (see the Discussion section).

Within the 0.06–0.30 ug/g interval the variability (standard error) of selenium level among populations is randomly distributed around that predicted from the mean selenium level (Fig. 3.2; y = 0.00649 + 0.0384X). Twenty six and 28 populations had respectively greater or less variability than predicted, with three populations matching the predicted variability. Populations with mean selenium levels of <0.06 ug/g (n=12 populations) and >0.30 ug/g (n=3) were always found to have variability within the population that was less than that predicted by the regression. The pattern of variability is confirmed by the residual of the standard error (Appendix B. Fig. 1). Individuals in populations occupying low selenium environments (i.e. <0.06 ug/g) were not able to randomly uptake selenium at greater rates than other members of the population, indicating restricted selenium bioavailability. The sample of populations from high selenium environments (i.e. > 0.30 ug/*g*) is limited, but low variability is consistent with individual animals being unable to randomly avoid high selenium uptake, obliging high selenium levels.

A conspicuous discontinuity separates the 0.30 ug/g upper limit and the three supplemented bighorn sheep populations, suggesting that a high presence of selenium in western North America is surprising. A gradual transition occurs among populations at the lower $\leq$0.06 ug/g end of the interval until the lowest 4 populations. The lack of a discontinuity may reflect a continuum of selenium bioavailability, suggesting that low selenium presence is more typical on ungulate ranges in western North America.

Differences in selenium levels among populations are a function of the location of habitats occupied and not the species. Selenium levels did not differ among the seven ungulate species, when the five populations of the boreal ecotype of caribou and the three supplemented bighorn sheep populations are excluded from analysis ($F_{6, 70} = 1.96$, $R^2 = 14.35$, $p = 0.084$). Inclusion of these eight populations indicated a difference ($F_{6, 78} = 3.34$, $R^2 = 20.45$, $p < 0.01$) in selenium levels attributable to habitats occupied and demonstrated by bighorn sheep supplemented by human activity and the boreal ecotype of caribou (Fig. 3.3).

Ungulate species displayed the same pattern of wide variation of selenium levels within a narrow interval (Fig. 3.3) as found in ungulate populations in general. Species of ungulates where the number of populations sampled was large (i.e. $\geq$ 20 populations) consistently displayed populations distributed outside of the 95% confidence interval for that species (Fig. 3.3). However selenium levels (range, mid-point) observed and estimated (Table 3.1) for all unsupplemented populations of all species was always <0.30 ug/g and for some populations of all species <0.08 (Puls 1994) and <0.12 (Herdt and Hoff 2011) ug/g selenium level commonly used as a lower reference for domestic sheep.

Populations outside of the 95% CI (Fig. 3.3) were geographically clustered supporting published findings that selenium levels in individuals and populations are a function of the environment they occupy. Population means that may be unexpectedly low (<0.06 ug/g, standard error always less than predicted by regression Fig. 3.2) were geographically concentrated in southwest Alberta and the southeast British Columbia mountain ranges (three bighorn sheep populations), in eastern Washington (two elk populations, one moose population), central California (six mule deer populations) and the Olympia Peninsula in Washington (two mountain goat populations) (Fig. 3.4). Populations that exceeded the 95% CI of the species typically had $\overline{X}$ selenium level of < 0.20 ug/g or were geographically clustered. The three bighorn sheep populations with selenium levels exceeding 0.20 ug/g were all from Hells Canyon (Fig. 3.4). All mule deer populations exceeding the 95% CI were <0.20 ug/g. Only one elk and one mountain caribou ecotype population exceeded a population mean selenium level of 0.20 ug/g. The two mountain goat populations that exceeded 0.20 ug/g were both captive populations. Boreal caribou (n= 5 populations), an ecotype, tended to have higher selenium levels than all other species or populations except for supplemented populations of bighorns. The three supplemented bighorn sheep populations had the highest population selenium levels followed by four of the five boreal caribou populations (Fig. 3.1). Wide variation within a narrow interval characterized selenium levels within unsupplemented populations of ungulate species.

Selenium levels in all three bighorn sheep populations identified as large extreme values, were greater than that occurring in unsupplemented ungulate populations in general (Fig. 3.1), L&GR Mines (n=82, t=-62.1, p<0.001), SRC (n=82, t=-32.02, p<0.001), and Lostine (n=82, t=-41.9, p<0.001). Similarly these three supplemented bighorn sheep populations had greater selenium levels than what occurred in all sampled unsupplemented bighorn sheep populations (Fig. 3.3) in western North America (respectively: n=21, t=-31.1, p<0.001; n=21, t = -15.8, p<0.001; n=21, t=-20.8, p <0.001). Consistent with the difference in selenium levels between bighorn sheep from SRC and caribou from Chinchaga, the former had lower selenium levels than bighorn sheep from Lostine (DF = 89, t = -4.47, p< 0.01), which in turn had lower selenium levels than bighorn sheep from L&GR (DF = 266, t = 8.11, p <0.01).

Selenium levels in two bighorn sheep populations sampled on Alberta coal mines were higher than ungulate species (Fig. 3.4) using the same geographic locations but not occupying coal mines. Bighorn sheep on SRC (n=24) had higher blood selenium levels than the proximate mountain goats (n=10) on Caw Ridge (df=16, t=7.38, p<0.01) and the Prairie-Redrock mountain caribou (n=19) (df=36, t=12.83, p<0.01). Selenium levels did not differ between these mountain goats and caribou (df=27, t=-1.53, p=0.138). Bighorn sheep on L&GR (n=200) had higher blood selenium levels than south Jasper mountain caribou (n=8)(df=58, t=31.26, p<0.01). Supplementation of selenium during 1999–2006 increased selenium levels in the Lostine, Oregon population (Fig. 3.4) relative to the pre-supplementation period and a period of supplement cessation in 2002 (df = 32, t = -10.94, p<0.01).

Selenium bioavailability from specific habitats may be consistent over extended periods of time. Selenium levels did not change in four populations sampled at 15 year intervals, including two populations using native ranges in Alberta. Selenium levels were the same in the bighorn sheep population at Ram Mountain (df=40, t=1.50, p=0.142) in both 1986–87(n=51) and 2001(n=21). Likewise selenium levels in mountain goats at Caw Ridge did not differ between 1987(n=7) and 2002–03(n=10) (df=7, t=-1.37, p=0.214). In the supplemented bighorn sheep population at Lostine selenium levels did not differ significantly from 0.224 ug/g prior to supplementation (1982) and during a period when supplementation did not occur 20 years later in February 2002 (df=11, t=0, p=1.00). Selenium levels in bighorn sheep on the L&GR are unexpectedly high from 1999–2001 (population means of 0.65, 0.75, 0.44 ug/g) and remained so in 2012–2014 (population means of 0.48, 0.50, 0.45 ug/g), but were different (df=194, T=-6.26, p< 0.01).

Bighorn sheep relocated (n = 22) from L&GR to Nevada in February 2013 were resampled (n = 7) in January 2014. After 11 months on a new range the selenium levels in these bighorn sheep ($\overline{X}$ = 0.16, St. Dev. 0.0375) was less than when captured on the L&GR (df = 26, t = 12.92, p <0.01), and was within the 95% CI of unsupplemented bighorn sheep (Fig. 3.3). The change of environment reduced selenium levels to that typical of bighorn sheep and other native ungulates (Fig. 3.4). Additionally, bighorn sheep sampled on L&GR in February 2014 (n=24) had selenium levels not significantly different to that found in the bighorn sheep at the start of their 2013 relocation (df=41, t=1.75, p=0.09)(Fig. 3.4).

Individual animals with selenium levels of < 0.05 ug/g or >0.30 ug/g are expected to be rare in Alberta other than among bighorn sheep, based on the distribution of selenium levels projected from sampled animals (Fig. 3.5, Table 3.2). Bighorn sheep on native range in particular have low selenium levels, with approximately 60% projected to have blood selenium levels <0.05 ug/g. Conversely bighorn sheep on coal mines are projected to almost exclusively exceed the 0.3 ug/g level. Alberta exhibits highly contrasting extreme differences in selenium levels among bighorn sheep, depending on the population's use of native ranges or coal mines (Fig. 3.4).

Ungulate populations in western Alberta were found to generally have selenium levels that are within the 0.06–0.30 ug/g interval, at both the scales of population mean and among individuals within a population (Fig. 3.4). Exceptions were observed for bighorn sheep in some native ranges with relatively lower selenium levels and novel ranges resulting from human disturbance that had uniquely high selenium levels. Bighorn sheep populations from Hells Canyon corroborate the Alberta findings of both the level of selenium present in ungulates and the exceptional values in some Alberta bighorn sheep populations.

Discussion

A Safe Operating Space

Selenium levels within the 0.06–0.30 ug/g interval identify a safe operating space, allowing the system and limits to persistence to be understood (Rockstrom et al. 2009). Resilience science facilitates assessment of the quality of the system (Holling 1986, Curtin and Parker 2014). Interval bounds are thresholds occurring at the edges of a stability regime and providing warning that feedbacks may change causing a shift in ecological state (Holling 1986, Holling 1996, Folk et al. 2004, Peterson 2008, Walker and Salt 2012, Curtin and Parker 2014). Individuals within populations occurring in the 0.06–0.30 *ug/g* interval (Fig. 3.2) are not restricted in selenium intake nor obliged to ingest high levels of selenium. Populations with lesser or greater variation in selenium levels among individuals have respectively lesser and greater variability in selenium bioavailability among habitats.

Outside of the 0.06–0.30 ug/g interval, variability in selenium levels among individuals within populations is always less than predicted (Fig. 3.2), indicating individuals in these population were vulnerable to selenium deficiency or toxicity. At selenium bioavailability <0.*06* ug/g individual*s* are unable to randomly increase selenium uptake, consistent with low selenium bioavailability on all habitats. At selenium bioavailability >0.30 ug/g individuals are unable to avoid high selenium uptake, consistent with high selenium bioavailability on all habitats. Selenium bioavailability that approaches or is outside of interval bounds may indicate geochemical or herbivory processes that inhibit population vigour. These risks may be ameliorated by high quality environments or compounded by low environmental quality. Ecological resilience affected by interactions between selenium bioavailability and environmental quality, (Holling 1973, Holling 1986, Gunderson 2000, Carpenter et al. 2001) is expected to reduce as selenium levels in a population approaches or exceeds the bounds of the 0.06–0.30 ug/g interval. Ecological resilience is concerned with maintaining the existence of ecological function (Holling 1996).

The proximity of selenium level to the 0.06—0.30 ug/g interval bounds is the important measure, indicating the potential for ecological function to be changing (Holling 1996) from providing life sustaining functions to functions associated with selenium deficiency or toxicity that generate populations characterized by poor performance without apparent cause. The precise location of the threshold is of lesser importance because this may change with (1) differences in environmental quality and (2) non-linear response to changes in controlling variables (Holling 1986, Holling 1996, Carpenter et al. 2001, Biggs et al. 2012). Populations proximate to the bounds of the interval (Holling 1996, Walker and Salt 2012) should be examined in greater detail rather than just populations falling outside of reference ranges (Poppenga et al. 2012). Small changes near thresholds have disproportionally large effects (Scheffer et al. 2003, Groffman et al. 2006). Individuals with selenium levels near the high upper bounds measured in California (Poppenga et al. 2012) may have exhibited reduced vigor, obscured by proximate factors (Flueck et al. 2012). The approach of identifying interval boundaries informs our understanding of impending change (Holling 1996), allowing the opportunity to manage environmental quality (Walker and Salt 2012) that compensates for deficient or toxic selenium bioavailability.

Selenium levels from populations from across western North America support the view that the application of deficient or toxic concentrations derived from domestic animals to wildlife is a questionable and possibly dangerous exercise (Robbins 1985, Hnilicka et al. 2004, McKinney et al. 2006, Poppenga. et al. 2012). The lower and upper bounds of the 0.06–0.30 *ug/g* interval are both less than that recommended for domestic sheep by either Puls (1994; 0.08–0.50*ug/g*) or Herdt and Hoff (2011; 0.12–0.35 *ug/g*). Selenium levels of less than the lower bound recommended for domestic sheep by Puls or Herdt and Hoff were documented in respectively 28% and 50% of unsupplemented ungulate populations. Unsupplemented ungulate populations were never documented to have selenium levels that approached the upper bounds recommended by Puls or Herdt and Hoff for domestic sheep. Selenium levels in supplemented bighorn sheep always exceeded the upper bound recommended by Herdt and Hoff (2011), and the L&GR population also exceeded the more liberal upper bounds of Puls (1994).

The Need for Effective Management Standards

Skorupa's (2008) review of selenium standards proposed for the Great Salt Lake articulated the needs of an effective standard. Full protection obliges a standard with a no-effects concentration. A no observable effects approach is without merit because of the subclinical nature of effects, the survivor bias of sampling and the difficulty with reversing the effects of poor quality environments. The no-observable effects approach is not a scientific construct, but rather a philosophy that reflects the bias to impose risk on environmental values to minimize industrial obligations.

Pragmatic management is obliged because of: (1) emergent properties that result from interactions between selenium bioavailability and ecosystem components (Holling 1986, Walker and Salt 2012); (2) subclinical effects of selenium deficiency and toxicity (Hebert & McTaggart-Cowan 1971, Flueck et al. 2012); and (3) the narrow margin between beneficial and toxic concentrations of selenium (Trumble and Sorenson 2008). Interval breadth must ensure that the protection of environmental values is certain

(Skorupa 2008). Contingencies to accommodate potential or surprise effects (Lindenmeyer et al. 2010) are obliged because: (i) deleterious effects occur before acute response and (ii) environmental values cannot be incorporated in a general manner into analysis or interval determination. Errors may allow for the imposition of environmental stresses with consequences that are difficult to correct (Skorupa 2008), generating resilience counter to high habitat quality.

Environmental Control

Our findings support earlier conclusions that selenium uptake and bioassimilation is controlled by the environment (Fielder 1986, United States Department of the Interior 1998, Underwood and Suttle 1999, Flueck et al. 2012). These findings are: (1) there is no species effect on selenium levels in ungulate populations based on 85 populations of seven species (Fig. 3.3); (2) range location resulted in differences in selenium levels between caribou ecotypes (Fig. 3.3); (3) selenium supplementation increased selenium levels in three bighorn sheep populations to levels not otherwise documented in ungulates (Fig. 3.1, Fig. 3.3, Fig. 3.4); (4) ungulate populations at Ram Mountain Alberta, Caw Ridge Alberta and Lostine Oregon each had the same selenium levels at samplings separated by 15 -20 years. Selenium levels in the Lostine population changed directly with discontinuing and continuing supplementation, reducing to pre-supplementation levels with a discontinuance and elevating to earlier supplementation levels with the continuance of supplementation (Fig. 3.4); (5) bighorn sheep occupying supplemented habitat on L&GR had high selenium levels in two sampling sessions each of three consecutive years separated by 10 years (Fig. 3.4); (6) The Prairie-Redrock caribou and the Caw Ridge mountain goat populations using the same range and sampled in the same year had the same selenium levels (Fig. 3.4); (7) two bighorn sheep populations using human caused high selenium environments on L&GR and SRC had higher selenium levels than ungulates using adjacent native range on respectively south Jasper (caribou) and Caw Ridge (caribou and mountain goats)(Fig. 3.4) ; (8) bighorn sheep relocated from the high selenium environment of L&GR in winter 2013 to a range in Nevada showed a decline in selenium levels in winter 2014 to that typical of unsupplemented ungulates, while bighorn sheep on L&GR maintained the high selenium levels in 2014 (Fig. 3.4) and (9) access to low elevation environments with higher selenium bioavailability (Flueck et al. 2012) is supported by our findings (Fig. 3.3 and Fig. 3.4). (10) Additional to our results, selenium concentration increased with experimental supplementation, by bolus placed in the rumen or reticulum of free ranging mule deer (Flueck 1994), in rations of captive moose (Stephenson et al. 2001), by salt blocks for free ranging bighorn sheep (Idaho Fish and Game unpub.), and by sodium selenite injection to mountain goats (Robbins et al. 1985). Findings 3–8 are each based on a limited number of populations because of practical constraints to applying different treatments to a large number of populations.

Selenium affinity and antagonism to mercury and other heavy metals is associated with both selenium deficiency and amelioration of heavy metal toxicity, particularly of mercury, from burning coal (Berry and Ralston 2008, Flueck et al. 2012). Selenium supplementation in this study does not involve burning coal and elevated mercury presence has not been reported. However it is possible that high dietary bioavailability of selenium on L&GR and SRC may beneficially counter undetected mercury release from mined coal. Additionally, low selenium levels characteristic of high altitude environments (Flueck et al. 2012) and demonstrated in Alberta by our data (Fig. 3.4) and previous studies (Samson et al. 1989) may cause bighorn sheep or other ungulates (e.g. elk) to select for relatively higher selenium bioavailability. Wildebeest (*Connochaetes spp.*) select for phosphate rich vegetation during the wet season (Ben-Shahar and Coe 1992), and the loss of migration to relatively greater selenium bioavailability on low elevation habits may contribute to the failure of huemul (*Hippocamelus bisulcus)* to respond to restoration efforts (Flueck and Smith-Flueck 2011). However attraction to inordinately high selenium bioavailability may pose toxicity risks.

Acquisition of data that can define the selenium regime to which an ungulate population is exposed to and the associated risk from environmental change is a relatively simple and inexpensive exercise that can be readily incorporated into standard monitoring and assessment programs. Whole blood can be obtained by aerial or ground capture of ungulates in conjunction with collection of other biological information. Blood can also be collected from hunter-harvested animals by cardio-puncture immediately after death. Small sample sizes will inform of the selenium level in the ungulate aggregation that occupies a sampled habitat. In most cases any one sample will identify the relationship of the population to the 0.06–0.30 ug/g interval or any other standard chosen to provide context. This consistency reflects the overriding influence of the habitat on selenium levels in ungulates. Of course, wisdom dictates obtaining a confirming sample size, particularly if initial samples are near the interval bounds.

Our findings support other demonstrations that environmental quality may ameliorate the potential for selenium deficiency in ungulate populations (e.g. Flueck et al. 2012). Ungulates in western North America form a continuum with no difference between successive populations with mean selenium levels less than the 0.*30* ug/g interval bound to less than the 0.*06* ug/g interval bound until a discontinuity at extreme low selenium levels (n= lowest 4 populations). This discontinuity suggests the capability of environmental quality and scalar relationships (Holling et al. 2008) to mediate risk of state change following disturbance at selenium bioavailability <0.06 ug/g may be limited.

Ungulate population mean selenium level >0.30 ug/g is apparently rare and appears strongly associated with human-altered environments. Exceeding the 0.30 ug/g level was characterized by discontinuity among the three populations and with the continuous distribution at <0.*30* ug/g. This discontinuity is consistent with a change in stable state caused by self-organization in response to a disturbance (Holling et al. 2008). Supplementation such as provided the Lostine bighorn sheep population may constitute a disturbance of similar effect on selenium bioavailability as the geochemical changes resulting from surface mining. Selenium levels are high in all individuals in each population and at the population scale is unrelated to other ungulate populations. Selenium levels greater than recorded for any other populations, the lack of variability among individuals, and potential interactions with ecosystem components that are not co-evolved, suggests that these are high risk environments where ungulate occupancy should be minimized. The ability to distribute away from high selenium environments, even for short periods of time, may contribute to an environmental quality that allows populations to tolerate relatively high selenium bioavailability. Selenium dosages approaching fatal poisoning can be reversed if the selenium source is removed, although embryonic deformities and some tissue damage cannot be reversed (See United State Department of the Interior 1998 for references).

Selenium levels from live animals are a conservative estimate of the exposure to risks from selenium bioavailability because of survivor bias (United States Department of the interior 1998). The occurrence of relatively high selenium levels in individual animals must be considered in addition to the proximity of selenium levels to the interval bounds. For example 98% and 62% of 200 bighorn sheep sampled on L&GR during 6 sampling years had selenium levels respectively >0.30 and >0.50 ug/g. Three individuals exceeded 1.0 ug/g extending to 1.8 ug/g. High selenium levels are widespread among surviving animals supporting the assessment of high risk from selenium bioavailability as determined from the population mean. Alternatively, although 88% of individual animals in the SRC population had a selenium levels of >0.30 ug/g, no animals exceeded 0.50 ug/g. Although notable risk is documented at SRC, the degree is less than at L&GR.

At least one animal with selenium concentrations >0.30 ug/g occurred in 21 of the 67 ungulate populations with mean selenium levels within the 0.06–0.30 ug/g interval. These are examples of randomly higher selenium levels in some individuals within populations, and did not typify selenium levels in the populations. These populations tended to be geographically clustered, to include five bighorn sheep populations from Hells Canyon, ten mule deer populations from California and four caribou populations from Alberta.

Management Directions

The unpredictable, subtle or eruptive nature of selenium effects may be approached by managing for adaptability where selenium levels may be deficient or transformation where selenium levels are high (Salt & Walker 2012). Management to achieve resilience by improving habitat quality can be initiated on ranges occupied by populations that are approaching or outside of the safe selenium bioavailability interval. Emergent response to selenium levels may produce surprising results in some cases. In circumstances where ungulates persist in environments comprised of complex (connectedness) co-evolved ecosystem components, a higher tolerance to environmental extremes (Carpenter et al. 2001, Biggs et al. 2012, Curtin and Parker 2014) is expected. The apparent prevalence of environments with low selenium availability and persistent ungulate populations may represent qualities emerging from interactions between selenium bioavailability and environmental quality that includes co-evolved ecological components. The prevalence (60%) of selenium levels of <0.05 ug/g in individual bighorn sheep using native range in Alberta may be indicative of high quality environments with inherently low selenium presence. The paucity of populations with high selenium levels suggests that the occurrence of high levels of selenium bioavailability is a rare occurrence, often dependent on human actions.

Determination of selenium bioavailability risks or effects by directly monitoring ungulate populations is impractical except where acute toxicity has widespread lethal effects (Rucker et al. 2008, Rederstorff et al. 2006), consistent with “excessive reductionism” and proximate factors obscuring variability, causation and surprises. In cases of high selenium bioavailability the only course of action is to exclude ungulates from these higher risk habitats and therefore monitoring is without merit. Management actions to detect or respond to selenium levels that approach or exceed the bounds of safe operating space, including monitoring efforts that collect useful information, must incorporate the realities of (1) subclinical effects of deficient or toxic selenium bioavailability; (2) the emergent nature, and therefore unpredictability of interactions among ecosystem components including selenium bioavailability; (3) the survival bias of live sampling; and (4) the difficulty with delineating a demographic population identity.

The consequence of elevated selenium bioavailability because of human activities is well documented (Flueck et al. 2012, Lemly and Skorupa 2012). Highly elevated selenium bioavailability should be expected where the processes of hydrolization and oxygenation by excavation, breaking and surface deposition of long-buried rock occurs. Minimal occupancy periods including exclusion of ungulates from high selenium environments that resulted from human activity may be the most effective management to achieve no-effects. Monitoring of target biota to detect population response due to selenium level is unlikely to provide meaningful information in a timely fashion, other than potentially detecting the occurrence of catastrophic response due to acute selenium effects.

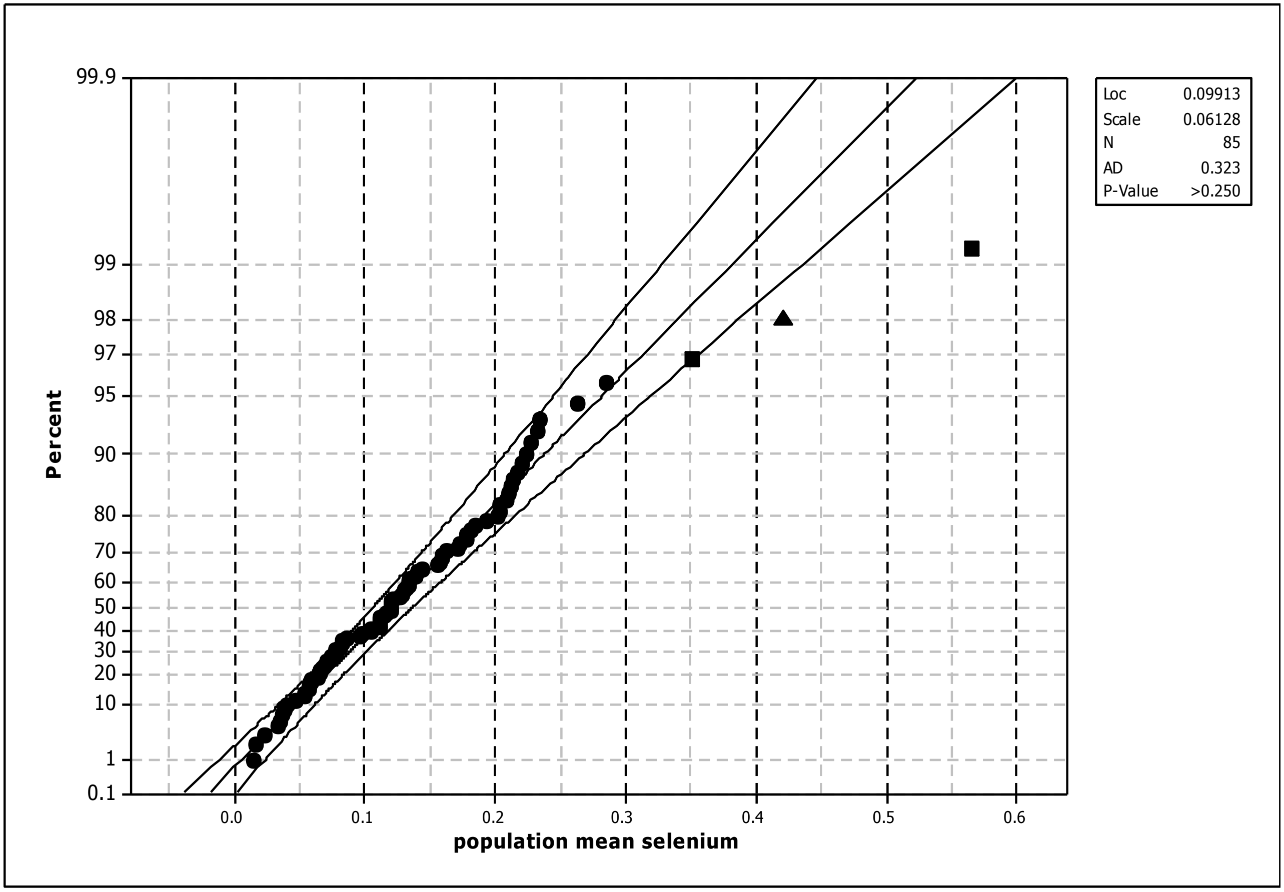
The apparently more common and geographically larger expanses of selenium deficient environments are a more difficult problem. Providing supplementation sources risks altering the ecologically important processes such as distribution and vulnerability to predation or spread of disease and may cause ecological or social concerns. A focus on enhancing environmental quality to reduce stress on selenium sensitive animals may be the most productive and possibly only effective management approach. The Ram Mountain experience at the 1986-87 sampling demonstrated that environments with low selenium levels can support high productivity ungulate populations. However this relationship did not persist to the 2001 sampling for unknown reasons that may or may not have been influenced by selenium bioavailability.

Conclusion

The ecological consequence of selenium bioavailability and determination of appropriate standards and management are important issues. Selenium levels in specific ungulate aggregations relative to the safe operating interval of 0.06–0.30 ug/g can be readily determined. A management focus on environmental quality is required to accommodate the subclinical effects of selenium bioavailability compounded by the interactive functions of ecological systems. If conservation is a management objective, monitoring to document a lethal or population level response to selenium levels is not responsible because populations are subject to adverse consequences without protective management. Informative local findings with respect to observed selenium levels that are relevant to this conclusion are included in supplemental information (Appendix B).

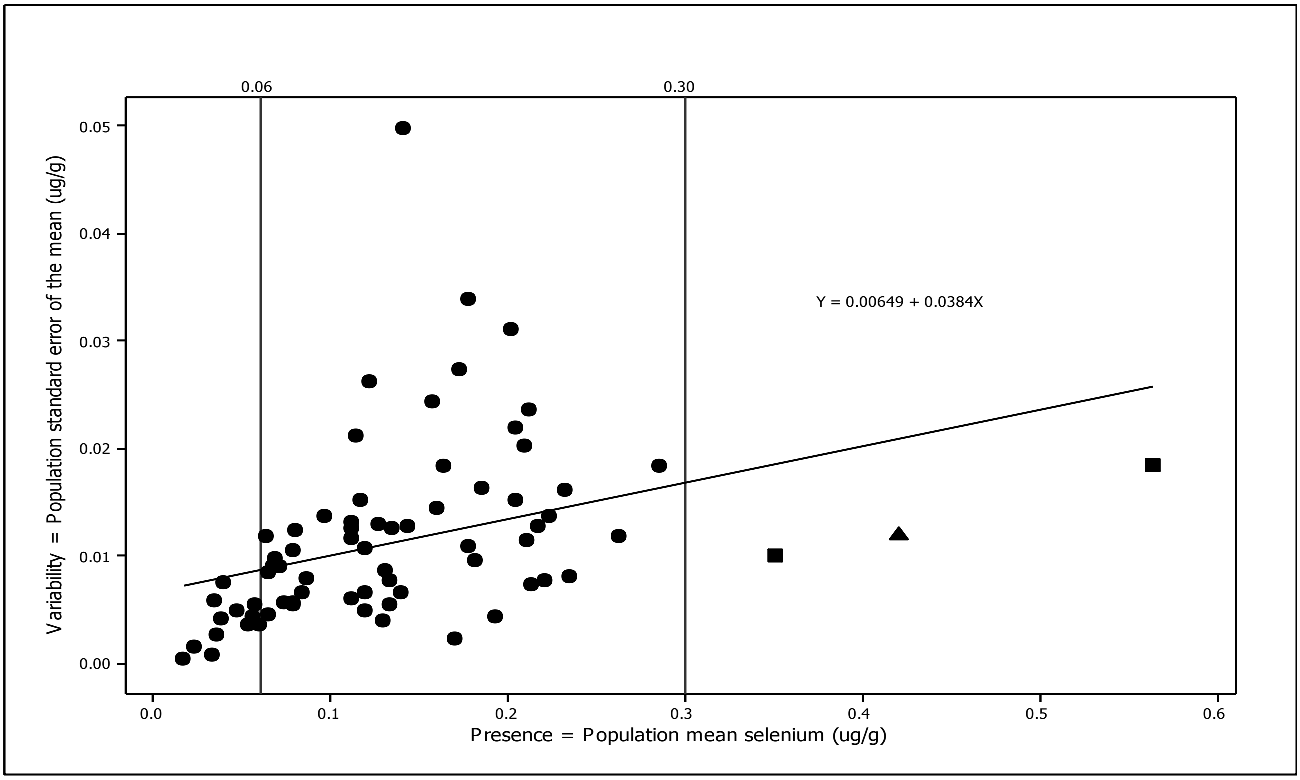
Addressing uncertainties associated with trace minerals such as selenium exemplifies emergent properties resulting from ecological variability and change that may be instructive to understanding other ecological processes and properties. A pathway to understanding other or broader ecological processes may be achieved through the examination of an interval measuring the resilience to changes in selenium presence and the influence of disturbance. Pragmatic management that enables persistence of ecological function (ecological resilience) is obliged to meaningfully accommodate the results of ecological interactions.

Fig. 3.1. Distribution of mean selenium levels in 85 populations of seven ungulate species including two caribou ecotypes in western North America. Anderson-Darling test determines the 95% CI of the expected distribution and the largest extreme values. Populations unsupplemented for selenium display a continuous distribution. Populations supplemented by environmental changes to geochemical processes (surface mining of coal) or purposely augmented, are discontinuous from unsupplemented populations and discontinuous among themselves, indicative of a disturbance caused difference in state.



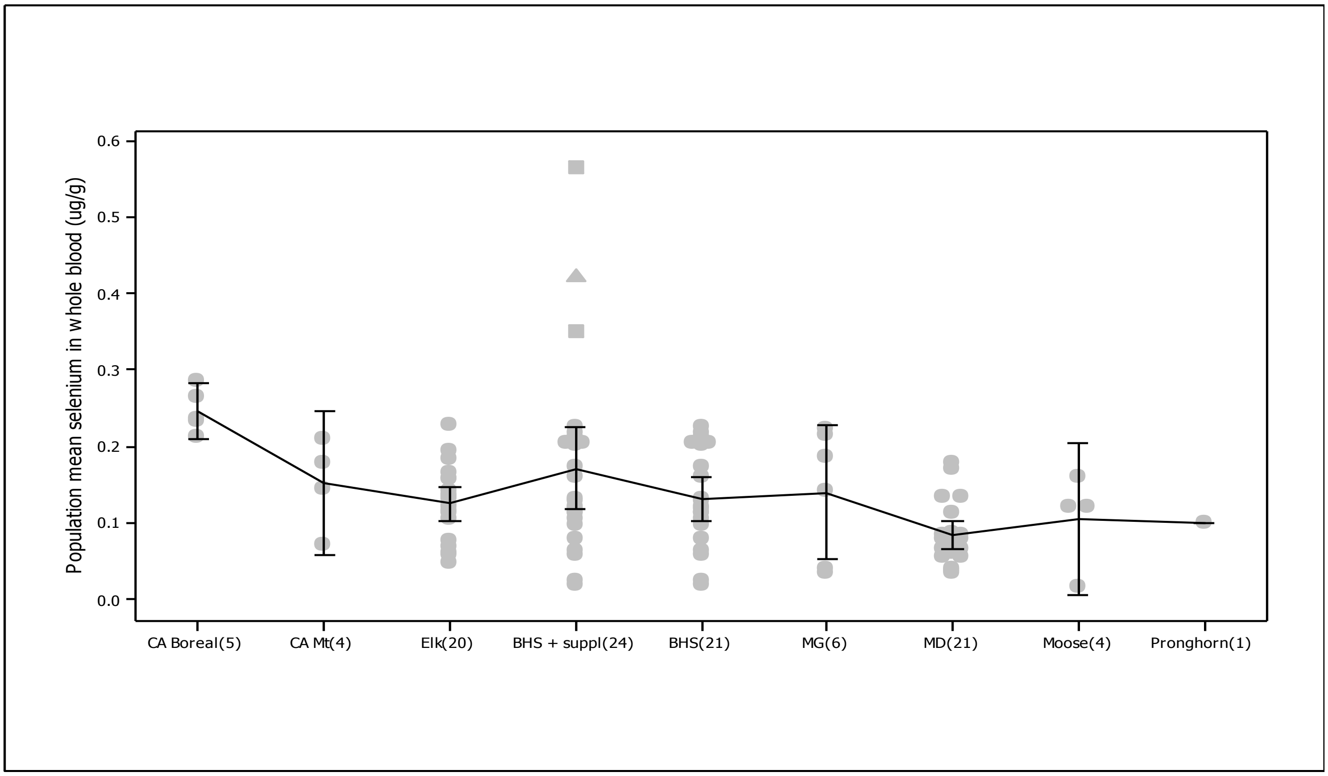
● = unsupplemented; ■ = coal mine; ▲ = purposely supplemented

Fig. 3.2. Identification of a safe operating space (0.06—0.30 ug/g) for selenium levels in western North America based on 72 populations of seven species including two caribou ecotypes. Outside of this interval the variability of selenium levels within the population is less than predicted by the regression, indicating restricted selenium bioavailability at <0.06 ug/g or obligatory high selenium intake at >0.30 ug/g.



● = unsupplemented; ■ = coal mine; ▲ = purposely supplemented

Fig. 3.3. Distribution of selenium levels in 85 populations of seven ungulate species including two caribou ecotypes in western North America. Distribution is for the mean of each species, showing the 95% confidence interval of the species. Populations occurring outside of the 95% CI for each species are geographically clustered (see text pg. 90) consistent with environmental control of selenium levels.

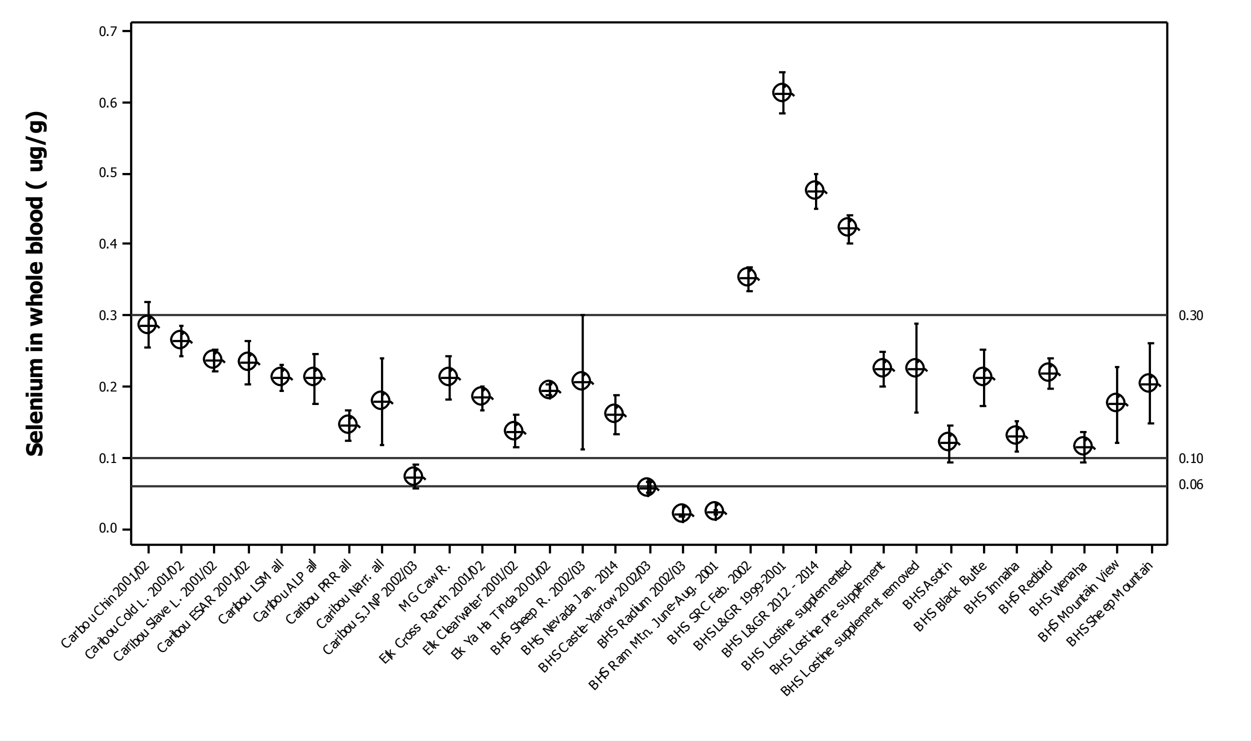


● = unsupplemented; ■ = coal mine; ▲ = purposely supplemented

Probability of a supplemented BHS population occurring among 21 unsupplemented BHS populations:
L&GR (n=21, t= -31.1, p<0.001); SRC (n= 21, t= -15.79, p< 0.001); purposely supplemented (n= 21, t= -20.8, p<0.001)

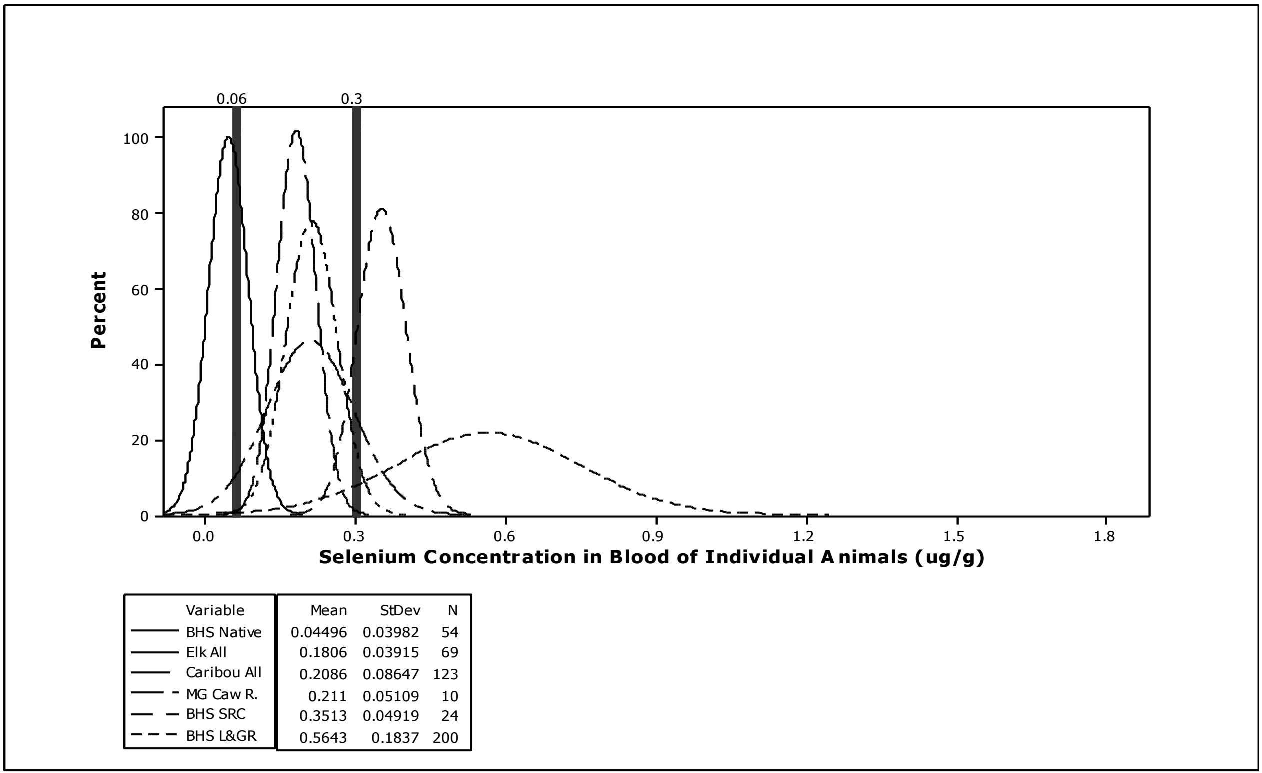
CA = caribou
BHS = bighorn sheep
Elk = elk
MG = mountain goat
MD = mule deer
Moose = moose
Pronghorn = pronghorn

Fig. 3. 4. Range of selenium levels in individual animals in 20 Alberta and 8 Hells Canyon ungulate populations at the 90% confidence interval. L&GR is presented as the two, three year sampling bouts (1999-2001, 2012-2014). Lostine Oregon displays the supplemented, pre-supplemented, and supplement removed selenium levels. SRC displays the 2002 levels relative to the Caw Ridge mountain goats and Prairie –Redrock caribou populations that occupy adjacent native range. (See text pg.96)



CI@90% to allow comparison with Poppenga et al. 2012

Fig. 3.5. Projected distribution of selenium levels in ungulates in Alberta based on whole blood od sampled animals, relative to the projected safe operating space of 0.06—0.30 ug/g.



Variable	Mean	StDev	N
BHS Native	0.04496	0.03982	54
Elk All	0.1806	0.03915	69
Caribou All	0.2086	0.08647	123
MG Caw R.	0.211	0.05109	10
BHS SRC	0.3513	0.04919	24
BHS L&GR	0.5643	0.1837	200

CA = caribou
BHS = bighorn sheep
Elk = elk
MG = mountain goat
MD = mule deer
Moose = moose
Pronghorn = pronghorn

Table 3.1. Measured range, 95% CI interval and estimate of mean selenium levels in whole blood in populations of ungulates in western North America.

Species	**Number of populations**	Measured Range ug/g		**95% CI of the mean ug/g**	
		Low-High	Breadth	**Interval**	**Midpoint**
Caribou – boreal	5	0.211 – 0.286	0.08	0.209 – 0.282	0.24
Caribou – Mtn.	4	0.072 – 0.210	0.18	0.057 – 0.245	0.15
Elk	20	0.048 – 0.227	0.18	0.103 – 0.148	0.12
Bighorn–unsupp.	21	0.017 – 0.224	0.21	0.103 – 0.161	0.13
Mountain Goat	6	0.035 – 0.222	0.19	0.052 – 0.228	0.14
Mule deer	21	0.034 – 0.178	0.14	0.067 – 0.103	0.09
Moose	4	0.015 – 0.160	0.14	0.005 – 0.202	0.10

Table 3.2. Projected normal distribution of selenium levels in ungulates in Alberta, in whole blood ug/g (n = sample size of individuals of each species the projection is based on)

Species - category	**n**	**<0.05 ug/g**	**>0.30 ug/g**
Mountain Caribou	54	<10%	<10%
Boreal Caribou	69	0	<15%
Elk	69	0	0
Mountain Goat	10	0	<5%
Bighorn Sheep native range	54	60%	0
Bighorn Sheep SRC	24	0	>80%
Bighorn Sheep L&GR	200	0	>95% up to 1.8 ug/g

Chapter 4.

Resilient Space – Implications for Management.

Introduction

Bighorn sheep (*Ovis canadensis*) population dynamics, including the influence of a novel environmental disturbance, were assessed at large spatial and abundance scales in the northern Rockies study area. Our interest is the ecological resilience of alpine species population dynamics over time in response to environmental variation, including disturbances. Resilience, a measure of persistence, is defined by tolerance to disturbance without changing self-organizing processes and structures (Holling 1973, Holling 1986, Gunderson 2000, Carpenter et al. 2001, Walker et al. 2004). Ecological resilience is concerned with the persistence of functions and desirability of state (Holling 1996), focusing on persistence of relationships among components and scales, changes in state and unpredictable response to disturbance (Holling 1996). Resilient systems and populations absorb disturbance and undergo change while retaining functions, feedbacks, structure and identity (Walker et al. 2004). Human-caused disturbances are expected to increase environmental variation (Boyce et al. 2006) and introduce novel environmental influences (Delibes et al. 2001, Battin 2004, Hobbs et al. 2009, Sih et al. 2011); challenging the ecological resilience of native ecological communities and constituent populations.

Dynamics of populations *("fast variables")* are strongly shaped by feedbacks among *"fast variables"* and with ecological variables linked to regulation of ecological conditions (*"slow variables"*) (Holling 1986, Biggs et al. 2012, Walker et al. 2012). Fast variables generate the dynamics of systems, and include population composition and distribution, and variation in vegetation productivity or moisture among seasons or years. Slow variables structure ecosystems and control processes, and include soil, topography, plant communities and hydrology. States of ecological systems and constituent populations are determined by ecological processes and structure. Wildlife populations are tolerant of, and may advantage from disturbances and environmental variability (Allen and Holling 2008) within a limited range, beyond which a change in dynamics, including a shift to an alternate stable state, may occur (Holling 1996, Scheffer et al. 2001, Holling 2008). Resilience science enables assessment of ecosystem and population response to natural and human disturbances (Walker and Salt 2012, Biggs et al. 2012, Curtin and Parker 2014). These responses are difficult to predict, and may be unpredictable, because of emergent properties and limited knowledge (Holling 1973, Doak et al. 2008, Lindenmayer et al. 2010, Curtin and Parker 2014), obliging assessment capabilities to direct systematic development, implementation, monitoring and revision of management programs.

Recognition of the potential to alter states and the occurrence of an altered state (Holling 1973, Holling 1986, Folk et al. 2004, Walker et al. 2004) is essential to meaningful management. The desirability of the state of the system or population determines the desirability of the current resilience (Walker and Salt 2012). Achieving desired state may require overcoming the resilience of an undesired state. A primary management question is resilience of what to what (Carpenter et al. 2001) (e.g. the resilience of alpine population dynamics to environmental variation).

The inherent ecological and social values of northern Rockies ecological systems and constituent populations provide a model to better understand tolerance and response to disturbance. The northern Rockies have expanses of limited purposeful human modification and re-disturbance. However, high altitudes are more susceptibility to climate change, and localized areas of human-caused highly modified landscape are present. Bighorn sheep winter composition and abundance measurements over the past 40 years are available to assess changes in populations and responses to disturbance. Contiguous habitat in the northern Rockies contrasts with characteristic fragmentation on more southern ranges.

Bighorn sheep horn growth annuli may capture the effects of annual environmental variations on bioenergetics. The genetics of bighorn sheep are relatively well understood allowing application to population structure and possibly population responses to environmental variation.

Our ultimate objective is to develop detailed management hypothesis, contingencies and a comprehensive monitoring program to enable the determination of status, and to influence structure and process at appropriate times. The geographic expanse and the probability of persistence of demographic populations can change in response to environmental variation, including human introduced drivers. Inherent limitations to predictability oblige managing for resilience. Primary constituents of the monitoring program are expected to be: (1) the state and variation in bighorn sheep population dynamics and vegetation productivity (fast variables) at defined times (2) association(s) among range segments and bighorn sheep cohorts (connectivity), (3) identification and testing of environmental variables that are structuring the system (slow variables) and (4) changes resulting from human demands for resource extraction and utilization (external drivers). Population and ecological management programs defined and substantiated from science based-management hypothesis, revised according to monitoring results, are expected to be the primary products.

Application of Results

Understanding relationships between population dynamics, connectivity and slow variables is a crucial initial management objective. Additional understandings of properties and processes may be gained if other ecological principles such as biodiversity can also be tested. These understandings will be most productive if properties and processes of sustainable ecological systems are applied within an appropriate governance structure (Biggs et al. 2012). Overriding governance questions are: (1) how do we know what the right thing to do is and (2) what is the right thing to do? Correctly conducting the intended action, commonly the test of management success, is only productive if the intended action is the right thing to do.

Management actions and understandings are treated as hypothesis, to allow for anticipation and detection of surprise, maintain objectivity and maximize opportunity to improve understanding and management (e.g. Lindenmeyer et al. 2010). This does not imply that management hypotheses are tenuous constructs; many are clearly factual. However, uncertainty will exist, at least due to emergent properties of complex interacting systems and unknowns. Identified uncertainties (unknowns) need to be acknowledged and discussed. Also, the existence of influential unidentifiable unknowns needs to be accommodated. Appropriate contingencies and management revisions will be required to accommodate novel and unpredictable population dynamics where disturbances change self-organizing processes and structures.

Population dynamics of bighorn sheep in the northern Rockies identify distribution from high productivity native ranges with decreasing abundances of rams or both sexes as the source of bighorns occupying novel range with low productivity and high increases in abundance (Chapter 2). Connectivity among range segments is important. We focussed on the large spatial and abundance scales but expect that there are finer scales of connectivity that are also important but currently not identified. The influence of a novel environment on large-scale distribution (Chapter 2) and exposure to novel environmental risk (Chapter 3) occurs in our study area. The application of genetic and genomic resources is expected to improve our understanding of connectivity. Depending on the degree of population structure in rams and ewes it may be possible to understand the influence of differences or similarities between the sexes and whether the relationship of ram natal ranges to location of death and to horn growth from birth to three to four years of age can be determined.

However, understandings of slow variables (e.g. soil composition, plant community structure, and hydrology) in the northern Rockies and the relationships to resilience and persistence of bighorn sheep is rudimentary. Population dynamics support a management hypothesis that the relatively undisturbed co-evolved ecosystem components are essential to persistence of the vigorous bighorn sheep population(s) currently occupying native range. The strong influence of novel environment on distribution, high probability of climate change influences (Tennant and Menounos 2013, Pollock and Bush 2013, Roberts et al. 2014, Zhuoheng and Grasby 2014, Pepin et al. 2015) and ongoing human alterations of landscapes suggest that external drivers will continue to modify slow variables, stressing bighorn sheep population dynamics (fast variables) and probability of persistence. Improved understanding of the relationships of slow variables to population dynamics and external drivers to slow variables, and management application of these understandings, are essential to successful management for bighorn sheep persistence and social benefit.

Environmental quality is most influential to species persistence (Holling 1973, Holling 1986, Carpenter et al. 2001, Walker and Salt 2012). Human-caused environmental changes are recognized as the ultimate influence on environmental quality (e.g. Alberta Bighorn Sheep Draft Management Plan (AEP 2015), Caribou Recovery Plan Alberta (ASRD 2004, Festa-Bianchet et al. 2011), Alberta Grizzly Bear Recovery Plan (ASRD 2008)). However, conservation initiatives for wildlife populations are commonly restricted to management actions that directly manipulate population composition or abundance of subject species, competitor or predator species. Administrative procedures intended to manipulate human-caused mortality (e.g. regulating hunting or illegal harvest, road management,) are the primary tools.

The presence of resilient populations that can absorb disturbance and change is dependent on management that delivers effective actions that appropriately affects slow variables and external drivers. Advantageous address of relationships between population dynamics (fast variables) and the system controlling slow variables and the pervasive influence of external drivers, well established in the literature (e.g. Chapter 1), can be impeded by governance. Administratively or culturally imposed constraints on management action are only explainable as protecting agency dogma (e.g. harvest manipulation can compensate for adverse environmental changes) or unstated mandate (e.g. deflect liability from resource extraction or consumption).

Immediate Technical Actions to **Implement**

1. **Establish or Estimate Population Identity.**

The sources and demographics of animals at a location define habitat quality (Schlaepfer et al. 2002, Bock and Jones 2004, Pulliam et al. 2011). The geographic extent of a demographic population can be approximated by successively aggregating adjacent bighorn sheep groups observed on proximate winter range until an adult sex ratio of ~65% females is achieved. To achieve a bighorn sheep aggregation mass representative of a demographic population, a minimum number of ewes (e.g. 125) needs to be assumed and tested. The proportion of lambs in demographic groupings estimated by adult sex ratio provides an estimate of the ability for these adults to support a persistent population (~20% lambs in total bighorn sheep). Comparison among these proxy demographic units may identify distributional stresses and dependency as have been identified in the northern Rockies. Management that addresses productivity (slow variables and feedbacks) and distributional stresses and dependencies (connectivity) can then be pursued, with the assurance that significant bighorn sheep abundance is subject to these productivity or distributional regimes even if there are inaccuracies in the determination of demographic populations.

Within the Northern Rockies each arbitrary native range census zone can meet the criteria for persistence of (1) ewes being ~65% of adults and (2) lambs being ~20% of total bighorn sheep. The novel habitat census zone in contrast exhibits abundance changes, adult sex ratio and lamb proportions consistent with a sink and a dependency on native ranges as a source. A proxy demographic population centered on bighorn sheep occupying the novel range of L&GR requires aggregating all bighorn sheep in the northern Rockies to achieve an adult sex ratio of ~65% ewes. This aggregation estimates a minimum area and population abundance required to support bighorn sheep on range segments with low reproductive and recruitment potential, identifying dependence on the productivity of the entire northern Rockies.

Difference between sexes in predisposition to distribute is consistent with the observed inverse relationship between ewes as a proportion of adults and changes in abundance. These changes allow for estimation of the capability to tolerate disturbance and the source of bighorn sheep occupying census zones with increasing abundances but low productivity. Within the northern Rockies these proxy demographic populations and an assumed lesser propensity for ewes to distribute identifies the entire northern Rockies and the Jasper and Cadomin census zones as respectively the source of rams and ewes that occupy novel habitat.

The conceptual connectivity and risk to source populations can be estimated as 450 rams and 450 ewes in the period of fall 2008–2011. Demographics support a management hypothesis that ewe distribution to novel habitat from the Cadomin and Jasper native range census zones constitutes a range shift of ~43% of ewes from native range since 1980. Demographics support a management hypothesis that 35% of rams have shifted range to novel habitat from all five native range census zones since 1980.

Contingencies consistent with awareness that the ram and ewe population structure within these proxy demographic units is unknown are required. For example a census zone may consist of two or more ewe genetic or demographic groupings, or a ewe grouping may overlap two or more census zones. A ram grouping may cover two or more ewe demographic groupings. In other words management must realize that a census zone meeting the persistence criteria is not necessarily independent of other census zones. Importantly the proxy demographic populations will allow for targeting and testing composition and productivity to better estimate geographic groupings that are consistent with population persistence.

Movement (connectivity) among range segments can be estimated from gene flow associated with genetically differentiated populations (e.g. Lowe and Allendorf 2010). The demographic population proxy generated by aggregating observed groups can be tested and refined by genetic populations identified from microsatellites not associated with traits bestowing fitness. We expect that ram and ewe genetic groupings will be differentiated. Spatial differentiation among ewe genetic populations and recognition of the distribution of rams relative to ewes is expected to be tested. Where greater differentiation is useful, mitochondrial DNA can be used to better distinguish ewe lineages or natal ranges of rams. The relationship of genetic groupings and demographics is expected to play an increasing role in identifying the source and geographic extent and state of populations, enabling more accurate understanding of connections and controlling variables at geographic and population scales.

2a. Maintain Connectivity Benefiting Populations.

Connectivity can advantage ecological resilience (Biggs et al. 2012) by distributing resources, providing sources for recolonization or providing alternatives to disturbed sites. Documented high population vigour on native range (Chapter 2) within the northern Rockies is hypothesized to include dependence on movement (I) among ranges of shifting quality at geographic scales smaller than ewe demographic populations, and (2) at larger spatial scales by the movement of rams among ewe aggregations. Hence management must achieve a high degree of physical connectivity among geographic units and sustain an array of biophysical units that have an adaptive cycle with stages that contribute to bighorn sheep persistence. By implementing a substantive landscape assessment program the influences, capabilities and connectivity of climate, topography and demands for resource extraction on slow variables (e.g. plant communities, soils) may be better understood, accommodated and advances in management of environmental quality for bighorn sheep achieved.

2b. Depress Access to Deleterious Novel Habitats.

Connectivity can be deleterious by spreading the consequences of disturbance such as disease (e.g. Besser et al. 2012) or attractive sinks (e.g. Donovan and Thompson 2001, Battin 2004) and expanding impacts (van Nes & Scheffer 2005). Connectivity will spread transmittable disease (i.e. pneumonia) adversely affecting population vigor of local aggregations of bighorn sheep (e.g. Cassirer and Sinclair 2006, Cahn et al. 2011) and if disease spread is to be controlled the density of bighorn sheep aggregations that can be tolerated may be limited. Bighorn sheep abundance, productivity and distribution are all expected to diminish if transmittable disease is established because connectivity will impose a resilience that is contrary to the persistence of vigorous bighorn populations.

Connectivity must also be managed to prevent significant use of attractive sinks by bighorn sheep. Attractive sinks likely occur at tolerable magnitudes and distribution on native ranges without the influence of human-caused landscape alterations. Demographic analysis (Chapter 2) did not identify attractive sinks within native range census zones that threaten the persistence of bighorns.

Demographic analysis demonstrated the presence of attractive sinks on novel ranges on surface mines. These sinks have the potential to deleteriously affect the entire bighorn sheep population in the northern Rockies. It is unknown whether the development of novel range expanded the geographic extent of distribution or enhanced holdover at a site in a traditional distribution pattern. Nevertheless these sinks exhibit a bighorn sheep composition in all fall or winter surveys from 1994- 2012 (n=31 including two winter surveys of Smoky River Coal Mines) that cannot support a population. These sinks are estimated to draw approximately 900 adults (equivalent to 26% of adults observed in the entire northern Rockies in the winter) from productivity generated by native range. This results in risk being placed on the entire northern Rockies bighorn sheep population because of (1) the magnitude of bighorn sheep abundance on sinks, (2) the dependence on distribution for the presence of bighorn sheep on sinks, (3) low productivity of bighorn sheep on sinks and (4) exposure of bighorn sheep on sinks to high levels of selenium and the possibility of subclinical affects.

Techniques to prevent bighorn sheep from occupying coal mines need to be explored, including: (1) Erecting fencing in early summer after the seasonal distribution of bighorn sheep to native range. (2) Relocating ewes and young rams back to source ranges if genetic analyses can make these determinations. (3) Ewes may be persuaded to stay on native ranges used in the summer by the use of herd dogs along the boundaries with coal mines. Large rams that reside on mines most of the year may not be able to be removed because of hoof or other conditions affecting physical fitness. (4) Restoration of disturbed landscape to native ecological units, consistent with an adaptive cycle that allows ecological resilience benefiting bighorn sheep and other native biota.

Existing native biophysical units at elevations of mine landscapes provide models to direct reclamation. Properly achieving restoration of the topographic and vegetation aspects of reclamation is hypothesized to reduce the probability of techniques one–three from becoming ongoing efforts. However, simplified novel locations proximate to high quality range are expected to remain attractive to bighorn sheep and because of that action to repel bighorn sheep is expected to be required prior to effective reclamation.

3**. Improve Understanding of Why Native Range is Highly Productive**

Meaningful efforts to conserve and sustainably exploit a wildlife population require understanding and management of factors determining environmental quality (Carpenter et al. 2001, Scheffer and Carpenter 2003, Walker and Salt 2012). Management hypotheses should focus on understanding the influence of salient slow variables on population dynamics and the characteristics of these slow variables (Biggs et al. 2012) and functioning of the adaptive cycle (Holling 1986, Walker and Salt 2012). Assessment of the status of populations and the cause of this status is dependent on understanding the structure of the ecosystem, processes causing change in this structure, and the influence of the resulting structure on population processes defining population state.

Environmental process and structure affecting bighorn sheep is poorly understood in spite of the recognized dependence of wildlife population vigour on environmental quality (Carpenter et al. 2001, Walker and Salt 2012). Improvements in this information and its application to ecosystems supporting bighorn sheep are a priority. However, the specificity of addressing this need is presently limited by the rudimentary knowledge of how these ecosystems function, influence of emergent properties and possibly agency dependence on excessive reductionism (Curtin and Parker 2014).

Managing for environmental quality to provide resilience for populations subject to stresses caused by increasing environmental variation changing structure and processes (Walker and Salt 2012) is dependent on understanding and maintaining ecological function (Holling 1996). Human activity is at least partially responsible for increasing environmental variation (Boyce et al. 2006). Vegetation patterns; relationship of these patterns to topography, hydrology and soils; and the influence of climate on these relationships are topic areas of present concern. Expanding shrub communities, snow condition, snow mass and duration and the extent and persistence of snow beds are hypothesized as significant controllers of bighorn sheep population dynamics. Investigation can be implemented and management hypothesis testing initiated within a few years.

4. Identify Safe Operating Space

Ecological resilience is concerned with the maintenance of function resulting from the interactions of complexity and disturbance (Holling 1996). Safe operating spaces (Rockstrom et al. 2009) present opportunity, depending on the state of habitat or population quality, to maintain functions and current resilience, or alter functions and resilience to achieve a state change. Surprise and the inherent variability of ecosystems, both of which are expected to increase due to human induced changes (Boyce et al. 2006), may be accommodated by safe operating spaces. Safe operating spaces can incorporate the cumulative effects of small changes (Scheffer et al. 2001), inform understanding of impending state change and oblige distance from state transition. A management framework is recommended that employs safe operating spaces to focus on (1) persistence of relationships, (2) changes in ecological and population processes and states and (3) the unpredictability of the consequences of disturbance and change.

Safe operating space thresholds provide useful direction and awareness of proximity to a state change (Scheffer et al. 2001), but are non-intuitive. Therefore, specific monitoring questions and methods and cautionary management is required to avoid approaching thresholds, if the current resilience is to be maintained. Equal caution is required where current resilience is intended to be overcome because of the emergent properties of change, particularly when induced by an external driver that is not a co-evolved ecological component (Carpenter et al. 2001). Measurement of threshold approach or exceedance may simply be academic verification of the state change. Point-specific thresholds are difficult and may be impossible to define because of the non-linearity and changeability of interactions among ecosystem components and scales. At or near thresholds, small changes or stresses can have proportionally large effects on state (Scheffer et al. 2001). These limitations highlight the risk that systems will be pushed to and beyond thresholds before appropriate attention to the consequences (e.g. woodland caribou *(Rangifer tarandus caribou)* in the study area) is given. Thresholds must therefore be treated as a dynamic construct undergoing continual testing, within a management framework that recognizes and accommodates the associated uncertainty. Proponent or governance position respecting approach to thresholds of safe operating space may reflect bias towards increased disturbance and influence of external drivers or maintenance of self-organizing processes that maintain ecological systems supporting bighorn sheep and associated ecosystem values and services.

We have identified two demographic (Chapter 2) and one trace mineral (Chapter 3) functional thresholds that have immediate management application as safe operating space. Management objective and direction to remain distant from functional thresholds needs to be explicit, unless a state change is the goal. Changes in adult sex ratio moving towards 60% or 70% ewes, or lambs diverging significantly from 20% of total bighorn sheep should produce a management response to determine if a distributional change is occurring in a demographic grouping or a range segment, or if there is some inordinate skew in mortality between sexes or ages. Such a skew could result from differences in habitat selection or changes in propensity of rams and ewes to distribute. Ungulates exhibiting selenium approaching 0.30 ug/g in whole blood should be excluded from ranges that consist of broken parent material that has been hydrolyzed and oxygenated by industrial activity. This finding is even more significant in Alberta mountain systems where selenium presence in ungulates is typically <0.10 ug/g. Management frameworks should focus on excluding wildlife from exposure to elevated selenium or improve habitat quality to increase tolerance to low selenium availability (<0.06 ug/g).

<u>Larger Scale Actions</u>

1. Management Focus on Connectivity and Slow Variables to Enable Understanding of Population Dynamics

Effective management of wildlife populations hinges on actions that affect the land and other ecological variables that structure ecological systems that species dynamics and persistence are dependent on. Co-evolved ecological components are recognized as most advantageous to wildlife species (Carpenter et al. 2001). Novel environmental features, particularly those resulting from human activities, may not be consistent with species persistence, particularly where the desired state is not highly resilient to environmental change (Walker and Salt 2012). Consequently, harvest-based population management, typically engaged in by wildlife agencies, cannot effectively accommodate environmental variation to provide for wildlife population persistence. Nor can population management compensate for inappropriate ecological management. Effective management will need to focus on ecological properties and processes associated with connectivity and slow variables and feedbacks (Biggs et al. 2012)

2. **Manage for System Complexity to Achieve Ecological Resilience**

The complexity of ecological systems is fundamental to advantaging from and tolerating environmental variation including disturbances (Holling 1986). Complexity is critical to understanding resilience (Curtin and Parker 2014); including tolerance to the nature or magnitude of novel disturbance (Carpenter et al. 2001, Walker and Salt 2012). Reorganization following a system-altering disturbance is the most probable phase for a shift to an alternate stability regime (Holling 1986, Carpenter et al. 2001, Walker and Salt 2012, Curtin and Parker 2014).

Ecological systems have been simplified to accommodate industrial extraction of resources within the northern Rockies and adjacent landscapes. Simplification is exemplified by the residue of surface mines colonized by bighorn sheep at density, composition and behavioural patterns inconsistent with a complex resilient system (Chapter 2). Agency response has been management of population dynamics through relocation of bighorn sheep to address abundance (AEP data), and prohibition of public access to address liability for landscape residue and vulnerability of behaviourally altered ungulates to harvest (GOA 2013). However, this management obscures, perpetuates and possibly exacerbates the sink effect and the reduction of resilience that mining residue has on northern Rockies bighorn sheep.

The standard management practices for caribou in the northern Rockies are a further example of the ineffectiveness of population management to compensate for ecological deficiencies. Caribou within and adjacent to the northern Rockies are categorized as threatened or endangered (Festa-Bianchet et al. 2011), primarily due to industrial alteration of landscapes (see Hervieux et al. 2014 for synopsis). Management focus on the proximate cause of mortality and apparent competition by respectively removal of wolves (*Canis lupus*) and ungulates failed to recover caribou (Hervieux et al. 2014). Most importantly, no evidence has been presented that an ecological system supportive of caribou persistence, including tolerance to disturbance has been achieved by attempts to manipulate population dynamics (fast variables) rather than focussing on slow variables and feedbacks.

3**. Novel Range Restoration to Native Condition**

Restoration of disturbed lands to native condition is expected to increase resilience to regime shifts that may result from landscape industrialization (Boyce et al. 2006, Walker and Salt 2012). Human activities alter landscapes in a manner directed by economically advantageous resource extraction. Industrialization has or is expected to cover large portions of lands supporting native wildlife populations. Through processes of connectivity these disturbances are expected to also affect non-industrialized lands including protected areas. The resulting biophysical unit may reduce tolerance of native wildlife to disturbance by removing resources or adding risk, including attraction (Delibes et al. 2001, Battin 2004, Hobbs et al. 2009, Sih et al. 2011).

4. Administrative Boundaries Defined by Ecological Boundaries

Administrative boundaries have a powerful influence on how ecological systems are managed. Management can unintentionally-effectively assume that administrative bounds capture ecological units which may result in ecological management becoming an artifact of clerical process. Within Alberta there are several examples of this that are applicable to bighorn sheep:

A) Bighorn sheep in Jasper National Park, a federally administered space, have until recent years been treated as demographically separate from bighorn sheep occupying Alberta. This administrative construct prevented recognition of the now documented dependency on connection and distribution to colonize coal mines in the L&GR census zone. The ecological relationship and management of these two range segments remains defined by administrative boundaries.

B) Bighorn sheep on coal mines have been inventoried and proclaimed as separate from bighorn sheep on native range. Coal mine boundaries are legal descriptions generated to accommodate administrative needs. Management actively treats bighorn sheep on coal mines as separate from those occupying native range in spite of bighorn sheep composition in all fall and winter surveys of L&GR documenting dependency on emigration from native range. Bighorn sheep specifically rams, on coal mines were not considered in the analysis of reduced hunter harvest of rams in Alberta (Festa-Bianchet et al. 2014), leading to potentially flawed support for conclusions and questioning of management agency and scientific credibility. Relocations to suppress abundance of bighorn sheep were conducted, possibly magnifying the sink effect of attraction to simplified habitats on coal mines, and again challenging management agency credibility.

C) Bighorn Species Management Areas (SMAs) are based on major drainages perceived to capture all significant bighorn sheep movement and assumed to define demographic populations. This administrative construct does not adequately accommodate the possibility for bighorn sheep crossing major drainages or any difference between sexes in propensity to distribute. Greater propensity of males to distribute explains the excessive abundance of rams on coal mines near Cadomin. Recognition of the possibility of ram movement from south of the Brazeau River to L&GR was inhibited by administrative boundaries. Consequently, contrary to all available data, bighorn sheep occupation of coal mines has been characterized and communicated as highly productive with high survival.

D) Administrative boundaries (Land Use Framework) for operational management of natural resources in Alberta are defined by large watersheds (e.g. Peace River, Athabasca River and North Saskatchewan River). These boundaries treat adjacent head waters lands that are ecologically indistinguishable but in different large river drainages as less similar, connected and interdependent than the headwaters and the mouth of each large river drainage. Bighorn sheep ranges are restricted to headwaters, regardless of the drainage. Accommodating the clerical demands of the administrative system effectively trumps and may preclude management for ecological state and persistence of resource values.

Relevant to bighorn sheep in the northern Rockies, the headwaters of major drainages fall into three different administrative regimes, creating a clerical separation of the management of ecological structure and processes. The separation between the Athabasca River and the North Saskatchewan River has existed since Alberta became a province because of federal administration of national parks, and is not subject to revision. The administrative separation of bighorn sheep range between the Athabasca and Peace Rivers is an entirely new construct imposing risks already documented in points A), B) and C) on ecological state, including bighorn sheep persistence, to accommodate clerical process. This risk can be readily removed to improve the probability of maintaining ecological resilience benefiting bighorn sheep.

Conceptual Framework

A conceptual framework to apply ecological resilience theory, concepts and empirical support to management of bighorn sheep populations in the northern Rockies is presented (Fig. 4.1). The framework intends to accommodate and where possible identify complexity, controlling processes and structure. The framework foundation is a panarchy encompassing connectivity and complexity that determines an environmental quality, which yields resilience sustaining or shifting the stable state. Interactions within the panarchy will affect self-organization in response to disturbance and regeneration. Unexpected results, including surprises, will occur at times and situations. Remaining within safe operating spaces may accommodate achieving a desired stable state, the uncertainty inherent in all dynamic systems, and provide the flexibility for pragmatic management in response to improved understanding and objectives.

Environmental processes are critical influences on population processes and state. Because of that achieving desired state requires that environmental processes are a management priority. The management schematic in Fig. 4.1 outlines relationships among **environmental** and **population vigour** and **external drivers**. **Demographic** measurement is essential to understanding **population state**. Environmental quality and population vigour both include substantial elements of uncertainty, particularly with respect to interactions. Environmental quality includes both fast and slow variables associated with biotic and abiotic constituents. Some feedbacks may occur, such as between vegetation communities and snow pack or snow bed duration, influencing fast variables among years and the state of slow variables such as plant community structure over longer time periods. Environmental quality results from the interaction of feedbacks, scales and structures that constitute the ecological context within which populations persist.

Demographic and distributional attributes display population vigour. Bighorn sheep population vigour is best measured by adult sex ratio and lamb proportion of total bighorn sheep abundance. Feedbacks and responses to the supporting environment determine population quality and the evolution of adaptive strategies and traits. Variation in response among individuals to environmental conditions is expected to contribute to population vigour and evolution. A complex of genes controlling fitness affecting traits, rather than a single or small number of genes, and the diversity of alleles for these genes, may contribute to resilience and tolerance to environmental variability and change (Miller 2015).

Variation in horn growth is expected to indicate annual variation in bioenergetics within a population, and persistent variation in bioenergetics among populations. The ability to vary the nutrients and energy that are contributed to growth of a tertiary structure (i.e. horns) is a measure of population vigour. The difference in the rate of horn growth among populations may not be meaningful to population vigour except in extreme cases.

Connectivity by distribution among habitats within a landscape may influence population complexity. Variation among habitats may advantage or disadvantage population vigour, amplifying or depressing the effects of disturbance. High quality environments are expected to contribute to resilience providing tolerance to risky disturbances and risky locations attractive to individuals. Risk may be contributed by (1) inherent aspects of the environment, or (2) novel habitats and features introduced by human modifications.

Complexity may differ with variation in distribution propensity and distances between sexes, among age classes or among population segments using different range segments. Rams relative to ewes and older rams relative to younger rams are expected to have a higher propensity to distribute and over greater distances. Bighorn sheep on the main ranges of the northern Rockies appear to display high complexity, at least for some range segments, while on the outlier range of Ram Mountain the species displays little population complexity. Connectivity is expected to facilitate feedbacks between the environment and the population, and within the population.

External drivers are significant natural or human imposed influences. The environment or the population respond to, but do not typically feedback, with external drivers. Feedbacks between external drivers and the environment may exist, particularly with governance. However, these feedbacks are not expected to fully compensate for the environmental or population response caused by the external driver.

Response to external drivers is expected to vary. Some external drivers are expected to produce very limited response (i.e. predator or competitor manipulation) and application may be a consequence of governance bias. However, extreme persecution or husbandry of individual species or trophic scales may cause ecological simplification that cause significant population response by bighorn sheep or other species, which is then amplified or depressed by feedbacks within the environment. Population response to hunting is expected to be trivial when sustainable harvest limits are applied in a high quality environment. However sustained persecution or callous disregard may cause an adverse response to harvest, particularly if amplified by a poor quality environment and /or unfavourable external drivers.

Governance has the potential to impose strong responses if biases or administrative boundaries and procedures cause change to processes and structures that control self-organization. Governance can manifest as active environmental manipulation, or passive treatment that may involve much action (e.g. dialogue, research) but limited application. A challenge to governance is when and how to act to advantage a desired stable state. Governance bias can impede determination of what is the right thing to do or how do you know what the right thing to do is.

Governance and resource exploitation are strongly linked. Both are external drivers of human origin that introduce novel disturbances and may increase the rate of change (Boyce et al. 2006, Sih et al. 2011). Disturbances from resource exploitation are commonly distributed widely through connectivity such as air, water, population movement or human commercial activities. Environment quality and population vigour respond to resource exploitation demands and economics, which may be geographically distant, and the approvals and operating standards that reflect governance bias.

Climate and weather establish the environmental context within which bighorn sheep must successfully adapt to, and respond to disturbance and regeneration. Feedbacks may occur among aspects of environmental quality, such as between vegetation communities and snowpack or snow bed duration, and population quality, such as distribution, amplifying or depressing the response.

Ecological simplification is the removal of the complexity that generates the tolerance that defines resilience. All of the categories of external drivers in Fig. 4.1 may contribute to ecological simplification. Ecological simplification is the cumulative consequence of external drivers and may incorporate some feedbacks with slow variables. Ecological, population and genetic simplification are all contrary to protecting the complexity that accommodates uncertainty and supports a stable state, including beneficial variation. However, at some point increased complexity is expected to cause adverse response or feedbacks (Holling 1986), limiting the benefit of complexity and justifying the application of a safe operating space.

Identification and accommodation of processes and scales that determine state are an objective of the management framework. Quantifying state is important but of limited value if the processes and the context that sustains complexity cannot be delivered in management. The management framework strives to identify the right thing to do and understand how we know what the right thing to do is. The ability to accommodate the uncertainty inherent in all ecological, economic and social contexts is a critical measure of management competency. Anyone can appear knowledgeable if they have all the data , however the true measure of knowledge is to be able to determine “rightness” when you run out of data (unknown).

Conclusion

Bighorn sheep populations in the northern Rockies are vigorous and the product of a high quality environment. This population state is being stressed by novel environments resulting from human disturbance and is likely prone to further stress resulting from climate change in high elevation environments. The resilience of the ecosystem to disturbance is being stressed by changes in ecological structure and processes. Opportunity is present to learn how this system functions, how to perpetuate the system and to restore ecosystem components that currently pose threat. These circumstances allow understanding and improved management to perpetuate bighorns and to benefit other wildlife species (e.g. caribou, grizzly bear (*Ursus arctos*)) and mountain ecosystems.

The inherent ecological complexity, structure and processes remain to perpetuate the system. Scientific understandings and methodologies exist or are emerging that enable management goals of achieving ecological resilience. However, the impediment of inappropriate administrative structure has been detected during the course of this study. Ecological management must become the goal of resource management agencies and administrative structure designed that facilitates environmental quality.

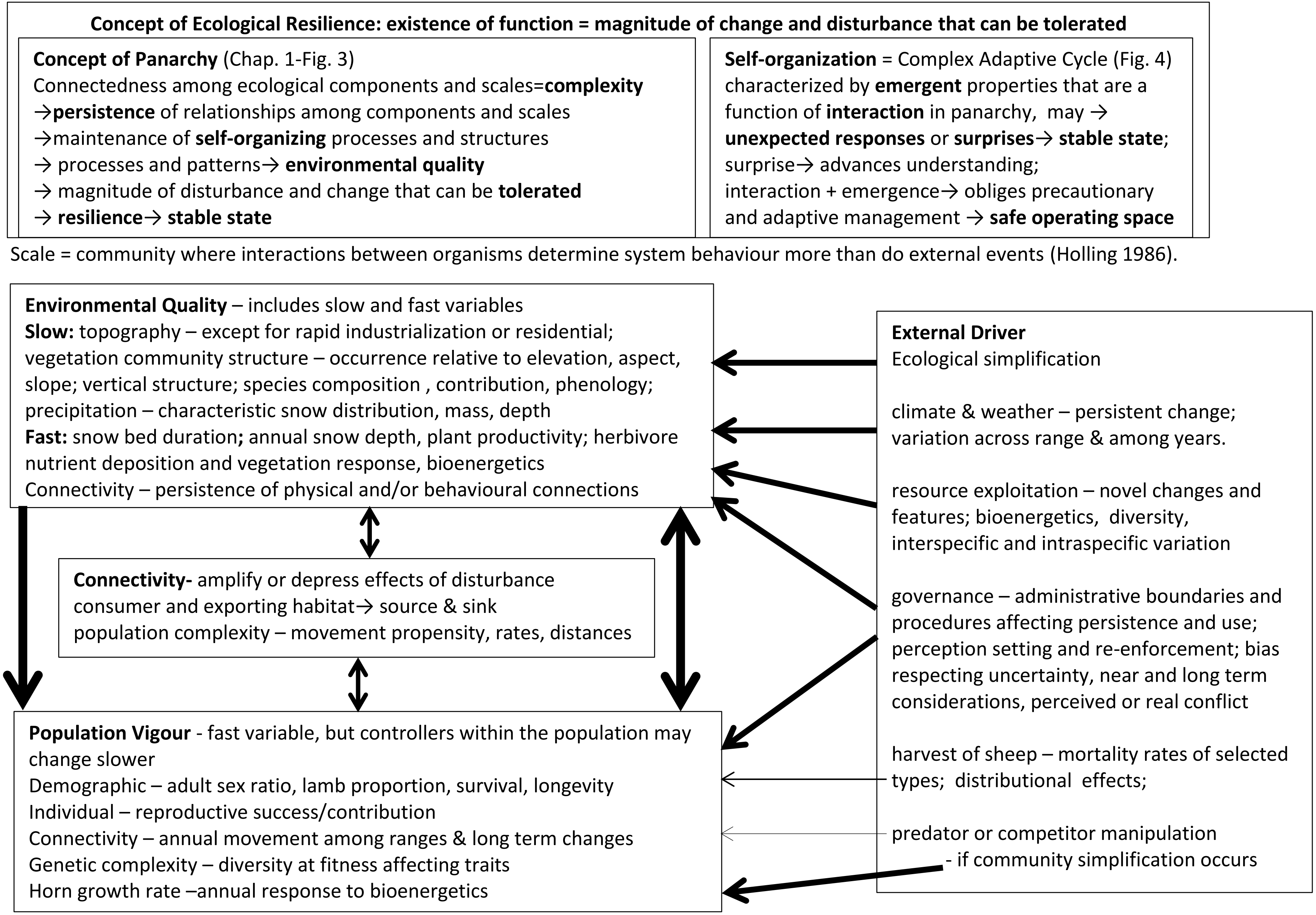


Fig. 4.1. Conceptual Framework to Apply Ecological Resilience - A Synthesis of Theory, Concepts and Empirical Evidence

Concept of Ecological Resilience: existence of function = magnitude of change and disturbance that can be tolerated

Concept of Panarchy (Chap. 1-Fig. 3)
Connectedness among ecological components and scales=**complexity**
→**persistence** of relationships among components and scales
→maintenance of **self-organizing** processes and structures
→ processes and patterns→ **environmental quality**
→ magnitude of disturbance and change that can be **tolerated**
→ **resilience**→ **stable state**

Self-organization = Complex Adaptive Cycle (Fig. 4)
characterized by **emergent** properties that are a
function of **interaction** in panarchy, may →
unexpected responses or **surprises**→ **stable state**;
surprise→ advances understanding;
interaction + emergence→ obliges precautionary
and adaptive management → **safe operating space**

Scale = community where interactions between organisms determine system behaviour more than do external events (Holling 1986).

Environmental Quality – includes slow and fast variables
Slow: topography – except for rapid industrialization or residential;
vegetation community structure – occurrence relative to elevation, aspect,
slope; vertical structure; species composition , contribution, phenology;
precipitation – characteristic snow distribution, mass, depth
Fast: snow bed duration**;** annual snow depth, plant productivity; herbivore
nutrient deposition and vegetation response, bioenergetics
Connectivity – persistence of physical and/or behavioural connections

Connectivity- amplify or depress effects of disturbance
consumer and exporting habitat→ source & sink
population complexity – movement propensity, rates, distances

Population Vigour - fast variable, but controllers within the population may change slower
Demographic – adult sex ratio, lamb proportion, survival, longevity
Individual – reproductive success/contribution
Connectivity – annual movement among ranges & long term changes
Genetic complexity – diversity at fitness affecting traits
Horn growth rate –annual response to bioenergetics

External Driver
Ecological simplification

climate & weather – persistent change;
variation across range & among years.

resource exploitation – novel changes and
features; bioenergetics, diversity,
interspecific and intraspecific variation

governance – administrative boundaries and
procedures affecting persistence and use;
perception setting and re-enforcement; bias
respecting uncertainty, near and long term
considerations, perceived or real conflict

harvest of sheep – mortality rates of selected
types; distributional effects;

predator or competitor manipulation
- if community simplification occurs

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Appendix A. Supplemental Demographic Information

Resilient Space: Bighorn Sheep *(Ovis Canadensis)* Demographics, Resilience and Response to a Novel Habitat in the Northern Rocky Mountains

Table 1. Pearson Correlations (r) Between Pre-rut Bighorn Sheep Presence on the L&GR Mine Complex and Late Winter Presence on the L&GR Mine Complex and Surrounding Native Range

Pre-rut Mine Category of Bighorn Sheep (n)=survey years	Late Winter Mine			Late Winter WMU 438 All = WMU 438 Native + 438 Mine			Late Winter All = WMU 437 + WMU 438 native + 438 Mine		
	r	R^2	p	r	R^2	p	r	R^2	p
Total Sheep (11) 1982-2011	0.950	0.903	<0.001	0.895	0.801	0.001	0.878	0.771	0.002
Rams (8) 1996-2011	0.880	0.774	0.004						
Ewes (8) 1996-2011	0.933	0.870	0.001						
Lambs (8) 1996-2011	0.739	0.546	0.036						
Lamb: ewe (8) 1996-2011	0.906	0.821	0.002						
Rams (6*) 1996-2011				0.837	0.701	0.038	0.807	0.651	0.050
Ewes (6*) 1996-2011				0.809	0.654	0.051	0.838	0.702	0.037
Lambs (6*) 1996-2011				0.544	0.296	0.265	0.603	0.364	0.205

Fig. 1. Change in Pre-Rut Total Ewes on Luscar and Gregg River Mines

Total Ewes = yearling ewes + >1.0 year old ewes

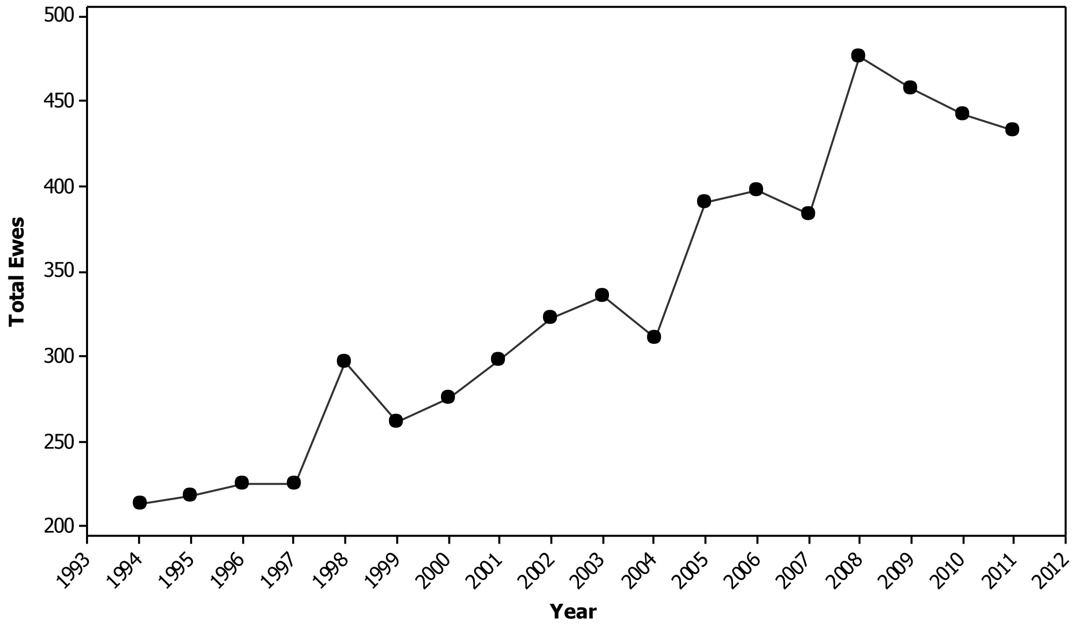


Fig. 2. Apparent Survivial Rates of Total Ewes and Rams Pre-Rut L&GR

Total Ewes = yearling ewes + >1.0 year old ewes

Survival Assumes L&GR is a closed population; growth is internally generated

Survivial Ratio = 1.0 yr. old in current yr. / yrl. + 1.0 yr. old in previous yr.

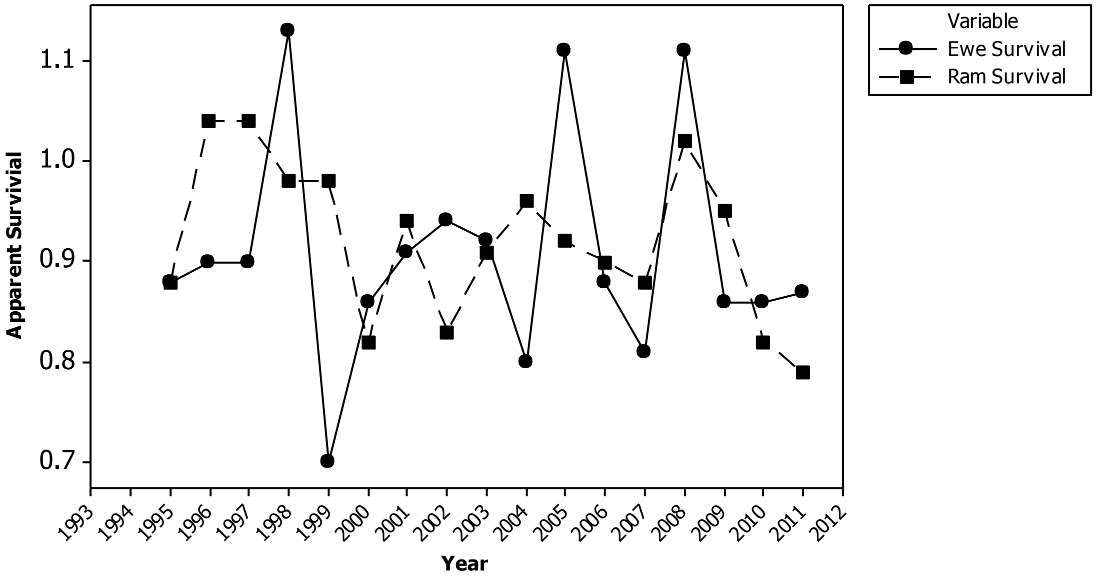


Fig. 3. Total Bighorn Pre-rut Abundance as a Proportion of Winter Abundance on Mines

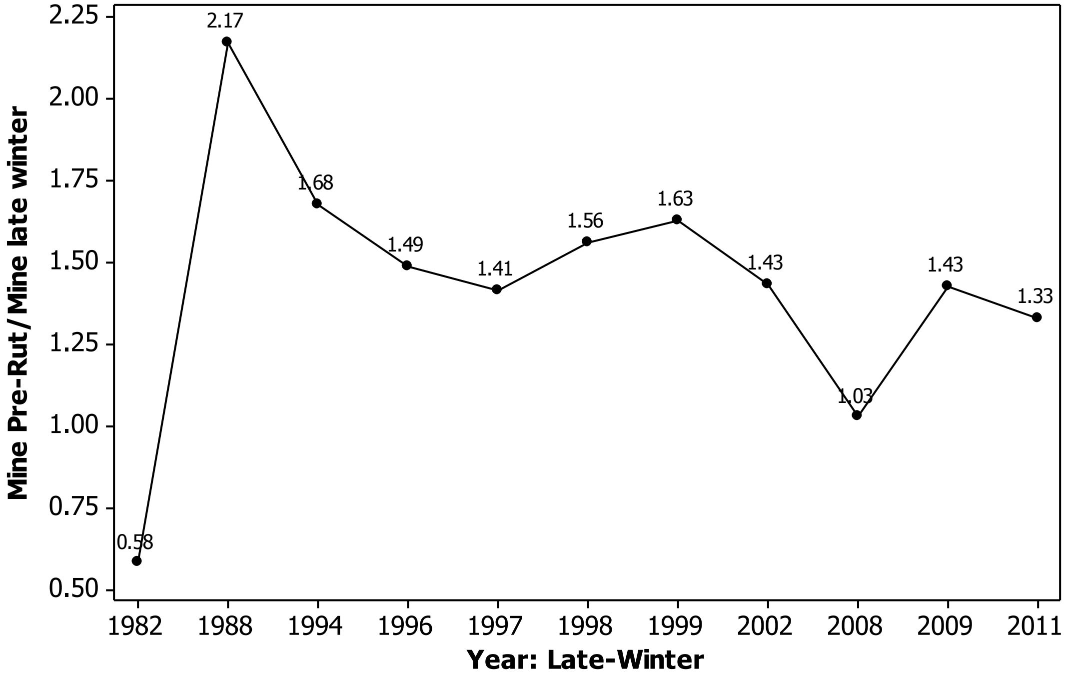
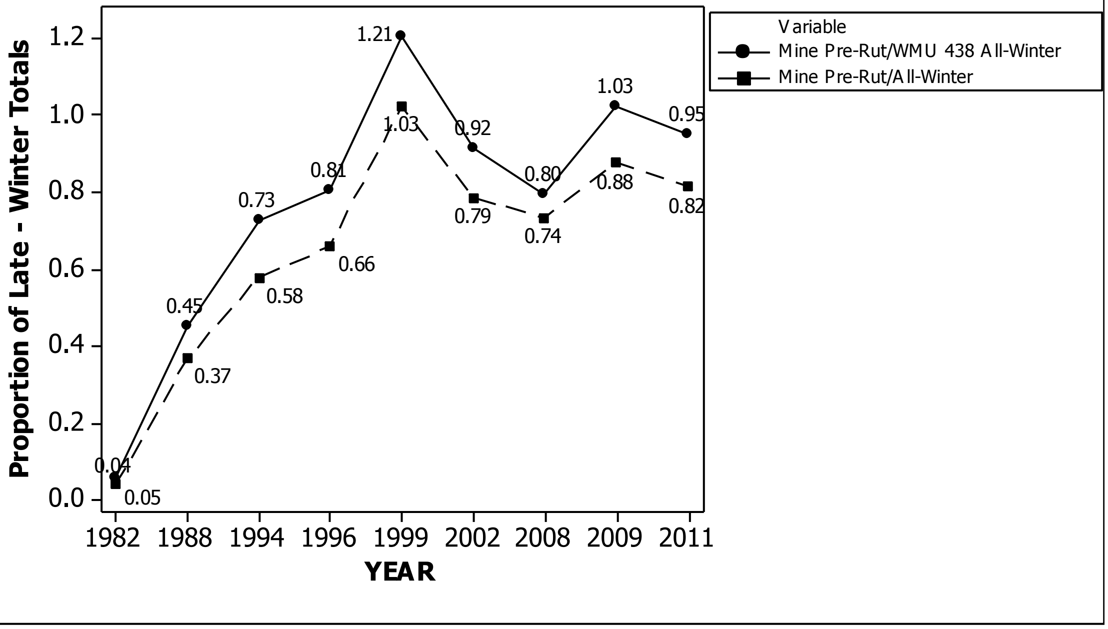


Fig. 4. Total Bighorn Pre-Rut Abundance on Mines as a Proportion of Winter Presence

WMU 438 All = WMU 438 Native + WMU 438 Mine
All = WMU 437 + WMU 438 Native + WMU 438 Mine



Supplemental Information:

Supplemental Table 1a. Changes in Bighorn Sheep Abundance and Composition in the Northern Rocky Mountains Late Winter of 1982 and 1983 to 2011. All ranges surveyed from 1980 to 2011

***- females as % of adults**

Year	Census Zone	Male	Female	Adult	Lamb	Total	Classified
1982/83	Clearwater 1982	265	413	678	170	955	848
	Nordegg 1980 (A)	82	235	317	88	419	405
	Jasper 1983 (B)	408	771	1179	360	1539	1539 (B)
64.9%*	Cadomin1982 less WMU 436	189	309	498	158	656	656
	Luscar & Gregg River Mines	9	22	31	12	43	43
	Willmore 1982 less WMU 446	262	500	762	238	1000	1000
	Total	**1215**	**2250**	**3465**	**1026**	**4612**	**4491**
1986-1988	Clearwater 1986	260	448	708	105	813	813
	Nordegg 1986	107	204	311	50	361	361
	Jasper 1987 (C)	408	771	1179	192	1382	1371
64.0%*	Cadomin 1988 less WMU 436 (D)	217	228	445	127	572	572
	Luscar & Gregg River Mines	40	47	87	33	120	120
	Willmore 1988 less WMU 446	170	438	608	173	817	781
	Total	**1202**	**2136**	**3338**	**680**	**4065**	**4018**
2011	Clearwater 2011	206	508	714	94	808	808
	Nordegg 2011	51	207	258	39	299	297
	Jasper 2011	298	421	719	167	872	872
64.7%*	Cadomin 2011 less WMU 436	174	244	418	125	555	543
	Luscar & Gregg River Mines	336	381	717	82	799	799
	Willmore 2011 less WMU 446 (E)	208	575	783	282	1070	1065
	Total	**1273**	**2336**	**3609**	**789**	**4403**	**4384**

A-data from 1980, 1982 data identified as large standardized residual, expect Banff sheep were on Nordegg ranges in 1982

B-unclassified survey, classification from 95% CI from all classified surveys of Jasper and other native range census zones (n=66)

C-south & central Southesk not surveyed due to wind; est. 100 sheep not reported, 2011 & 2012 surveys support the estimate

D-pilot issues, low count

E-WMU 445 data from winter 2010 (Dec. 2009)

Changes in ewe abundance on L&GR 1982- 2011 inversely correlated to changes in ewes on most proximate native range in Jasper (r = -0.998, p = 0.040) and Cadomin less WMU 436 census zones. (r = -992, p=0.078)

Changes in ram abundance on L&GR 1982-2011 inversely correlated to changes in rams on all native range census zones (r = -0.998, p = 0.043)

Small sample size of Jasper survey years inhibits determination of probabilities

Supplemental Table 1b Changes in Bighorn Sheep Abundance and Composition in the Northern Rocky Mountains Late Winter of 1982 and 1983 to 2011.
For 2011 includes WMU 436 in the Cadomin census zone and WMU 446 in the Wilmore census zone, and all other ranges surveyed from 1980 to 2011

***- females as % of adults**

Year	Census Zone	Male	Female	Adult	Lamb	Total	Classified
1982/83	Clearwater 1982	265	413	678	170	955	848
	Nordegg 1980 (A)	82	235	317	88	419	405
	Jasper 1983 (B)	408	771	1179	360	1539	1539
64.9%*	Cadomin 1982 less WMU 436	189	309	498	158	656	656
	Luscar & Gregg River Mines	9	22	31	12	43	43
	Willmore 1982 less WMU 446	262	500	762	238	1000	1000
	Total	**1215**	**2250**	**3465**	**1026**	**4612**	**4491**
1986-1988	Clearwater 1986	260	448	708	105	813	813
	Nordegg 1986	107	204	311	50	361	361
	Jasper 1987 (C)	408	771	1179	192	1382	1371
64.0%*	Cadomin 1988 less WMU 436 (D)	217	228	445	127	572	572
	Luscar & Gregg River Mines	40	47	87	33	120	120
	Willmore 1988 less WMU 446 (D)	170	438	608	173	817	781
	Total	**1202**	**2136**	**3338**	**680**	**4065**	**4018**
2011	Clearwater 2011	206	508	714	94	808	808
	Nordegg 2011	51	207	258	39	299	297
	Jasper 2011	298	421	719	167	872	872
65.2%*	Cadomin 2011	190	296	486	144	642	630
	Luscar & Gregg River Mines	336	381	717	82	799	799
	Willmore 2011 (E)	260	695	955	304	1265	1259
	Total	**1341**	**2508**	**3849**	**803**	**4685**	**4665**

A-data from 1980, 1982 data identified as large standardized residual, expect Banff sheep were on Nordegg ranges in 1982
B-unclassified survey, classification from 95% CI from all classified surveys of Jasper and other native range census zones (n=66)
C-south & central Southesk not surveyed due to wind; est. 100 sheep not reported, 2011 & 2012 surveys support the estimate
D-pilot issues, low count
E-WMU 445 data from winter 2010 (Dec. 2009)

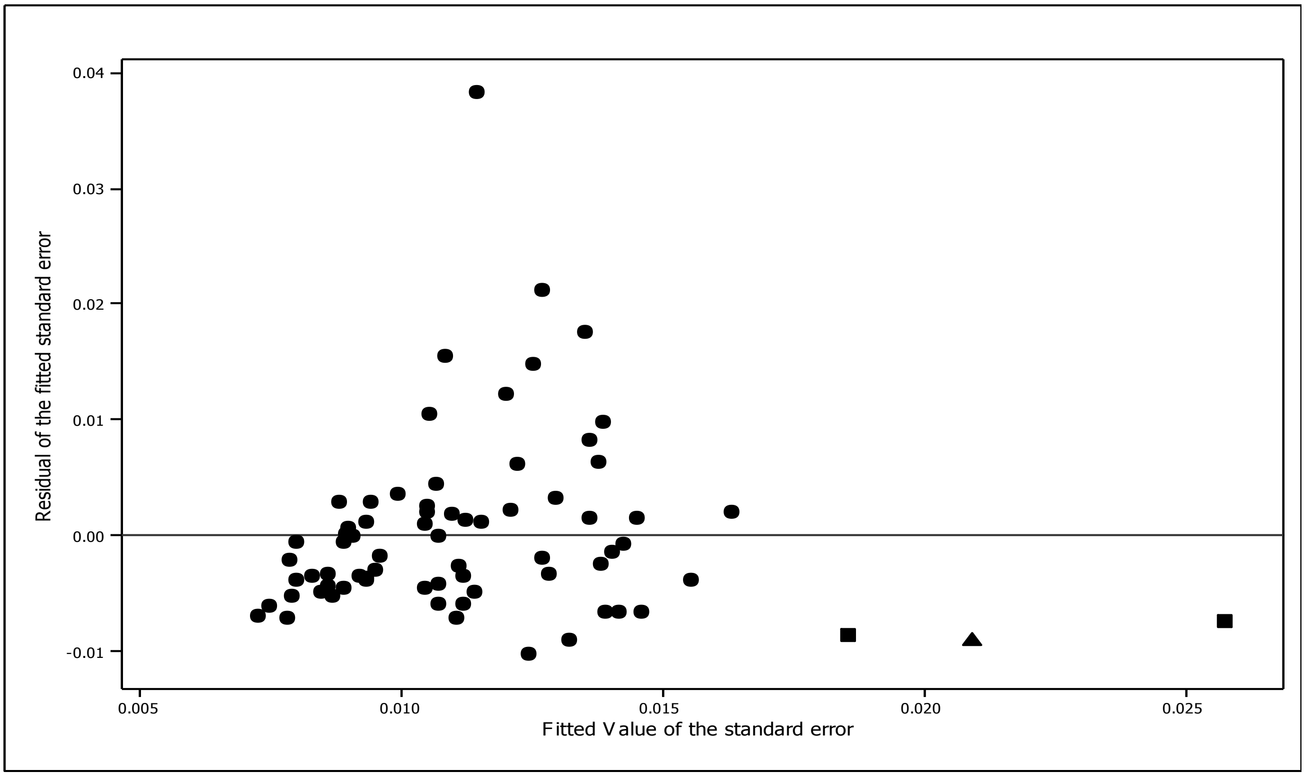
Supplemental Notes

Supplemental Note 1: In recent years, historical bighorn sheep range in WMU 436 (surveyed in 2011 and 2012) was added to the Cadomin census zone and in WMU 446 was added to the Willmore census zone (surveyed in 2009 and 2011). Results from the two surveys in each of WMU 436 and WMU 446 are corroborative. Therefore, the observed population estimate for the study area is increased by 68 rams (16 and 52 in WMUs 436 and 446 respectively) and 172 ewes (52 and 120 in WMUs 436 and WMU 446 respectively) for totals of 1341 rams and 2508 ewes (maintaining the 65% females adult composition) in winter 2011 (Suppl. Table 1b.). Additionally, an untested estimate of approximately 200 adult bighorn sheep is present on historical ranges (e.g. Wilcox Pass, Old Fort Point, Mile 3, Upper Rock-Deer-Mowitch Creeks, Ancient Wall, North Berland) not included in the surveyed areas.

Supplemental Note 2: The agreement of population abundance trend and magnitude of change between the 1982–2012 and 1980–2012 time periods for rams (Table 2.) and an opposing trend for these time periods relative to 1972–2012 is consistent with a lower rate of observation of bighorn sheep rams present prior to 1980. A stronger increasing trend in ewe abundance on native range census zones from 1972–2012 than in 1980–2012 or 1982–2012, including opposing trends in Cadomin (Table 2), also suggests a period of lower observation of ewes present in 1972–1978. The relatively low and high reporting of respectively ¼ curl and ½ curl rams in some surveys during the 1972–1978 period (Unpub. AEP data) further supports the hypothesis of a learning period

Appendix B. Supplemental Selenium Bioavailability Information

Fig. 1. Distribution of the residuals of the standard error of selenium levels based on 72 populations of seven ungulate species. The residuals distribute randomly within the 0.06—0.30 ug/g interval (safe operating space) consistent with the variability of the standard error of the mean to the regression predicted by the mean population levels (Fig. 2). Outside of the 0.06—0.30 ug/g interval the standard errors is less than the fitted value indicating restricted selenium bioavailability at<0.06ug/g or obligatory high selenium intake at 0>0.30ug/g.



● = unsupplemented; ■ = coal mine; ▲ = purposely supplemented

A number of significant local findings provide useful insight into selenium variability but are not fundamental to our thesis of safe operating space and environmental controls and mediation. The interaction of processes controlling selenium bioavailability and environmental quality limit predictability and the value of monitoring to detect risk before state change has occurred. Monitoring for direct effects to population vigor is not a responsible response to elevated selenium presence.

The relatively wide interval and high upper bounds of selenium levels in California bighorn sheep (Poppenga et al. 2012) may indicate use of a wide range of habitats, possibly including some human altered environments (e.g. irrigation, surface mining or livestock trace mineral supplementation). Unfortunately variances are not reported and results could not be incorporated with the 85 populations we used (Fig. 1, 2a, 2b, 3). Midpoints of reference ranges for six of seven bighorn sheep populations in California (Poppenga et al. 2012) were all >0.2 ug/g and <0.30 *ug/*g, consistent with the characteristic geographic clustering of populations with selenium presence outside of the 95% CI for species. The upper bounds of the 90% CI for 6 of the seven California populations exceeded the upper bounds of the 90% CI of 18 Alberta and eight Hells Canyon unsupplemented ungulate populations (Fig. 4). Upper bounds of 0.40, 0.43 and 0.49 *ug/*g were estimated for respectively three, one and one California population, exceeding any upper bounds estimated in unsupplemented populations in Western North America. The central tendency of selenium presence in California bighorn sheep was similar to that measured in boreal ecotype of caribou in Alberta. The relatively high selenium levels of California bighorn sheep is less than selenium levels in supplemented populations, supporting earlier evidence that selenium presence as observed in supplemented populations are rare, typically associated with human activities and should be considered risky.

Selenium is among an array of low profile environmental influences which may contribute to mysterious population performances (Flueck et al. 2012). These influences manifest through interaction with other environmental factors and are most suitable for understanding and management by application of concepts of ecological resilience. The Ram Mountain bighorn sheep population is an example of where mysterious population changes may be influenced by selenium bioavailability (Flueck et al. 2012). Selenium presence in Ram Mountain bighorn sheep is relatively low (n =72, $\overline{X}$ = 0.024 ug/g ± 0.01), displaying a bioavailability where selenium deficiency effects may occur. Selenium presence was the same when the population was highly productive (Samson et al. 1989) in 1987 (n= 51, $\overline{X}$ = 0.025 ± 0.01) and in 2001 (n= 21, $\overline{X} = 0.021$ ± 0.01) when the population was unproductive, had declined severely and could not tolerate predation (Festa-Bianchet et al. 2006); consistent with the subclinical effects of selenium deficiency (Hnilicka et al. 2004, Flueck et al. 2012). The cause of this change is unknown (J. Jorgenson per.comm.), although consequences such as density dependence and Allee affect are supported (Festa-Bianchet et al. 2014).

The rapid and persistent change in population vigor at Ram Mountain is consistent with a regime shift resulting from changes in environmental quality interacting with population dynamics (Holling 1973, Holling 1986, Scheffer and Carpenter 2003, Folk et al. 2004, Carpenter and Brock 2006). Interactions between a constant selenium presence and changed environmental circumstance may have produced feedbacks that changed population vigor and achieved resilience contributing to bighorns persisting in an unproductive state. Bighorn sheep populations occupying proximate native range not connected to Ram Mountain by the distribution of females did not exhibit this decline in population vigor (Chapter 2).

Difficulties in obtaining useful information on risks associated with selenium levels at or exceeding safe operating space because of subclinical effects, emergent properties, and survival bias are exemplified in the high selenium environments of the L&GR coal mines in Alberta and phosphate mines of southeast Idaho. Selenium bioavailability on L&GR is the highest recorded in ungulates that we are aware of. Selenium values not only exceed that of our proposed 0.06–0.30 ug/g interval, but also other possible safe limits (Puls, 1994, Herdt and Hoff 2011, Poppenga 2012). Emigration of bighorn sheep from a highly productive 42,000 Km^2 native range is responsible for bighorn sheep presence on the low productivity 40 km^2 novel ranges on L&GR (Chapter 2). Bighorn sheep abundance in the fall on L&GR is equivalent to up to 20% of all bighorn sheep adults observed in the winter on native and novel ranges (>3500 adults) combined. Bighorn sheep abundance on L&GR decreases in the winter (period of greatest nutrient and energy conservation) and is lowest in the summer (period of greatest nutrient and energy acquisition). Evidence of response to selenium would be obscured by subclinical effects, survivorship bias of sampling, emigration to L&GR, and seasonal distribution patterns. These constraints are consistent with the problem of proximate factors obscuring ultimate factors, resulting in determinations of no obvious evidence (Flueck et al.2012).

Prompted by selenium poisoning caused deaths on reclaimed phosphate mines, whole blood of domestic sheep analyzed weekly documented selenium levels in the range that may produce acute toxicity (Fessler et al. 2003). In spite of monitoring only detecting limited acute toxicity (one death from selenium toxicosis, two high to toxic exposure) these authors stated that additional deaths should be expected because of the high selenium environment. As predicted, 327 domestic sheep died on proximate ecologically similar range due to unexpected high selenium concentration in palatable forage not previously known to be an accumulator (Fessler et al. 2003, Pro-Med 2003). Similar die-offs have continued on these and other reclaimed lands. Emergent qualities associated with selenium presence and dynamic ecosystems limit the value of reductionism and data collection. Effective resource action and conservation can be impeded by excessive reductionism (Holling 1973, Doak et al. 2008, Curtin and Parker 2014).

Appendix C. Potential Management Scenarios for Testing the Scenario Approach

Management scenarios provide an understanding of possibilities, allowing integration of science with other disciplines to estimate consequences (Groffman et al. 2006) without the excessive reductionism (Curtin and Parker 2014) associated with pursuing definitive probabilities (Clarke et al. 2001). Scenarios allow examination of what might happen, identify potential controlling processes and structures, and develop potentially appropriate management. Scenarios build upon theory, concepts, empirical findings, perceptions and visions to generate circumstances that ought to be evaluated or accommodated. Evaluation may range from analysis of existing data and the literature to accommodation by direct application of management techniques assessed through pointed monitoring or initiation of research efforts. Application and assessment of a safe operating space is essential to accommodate uncertainty. The distance of this space from potential state changes (thresholds) becomes more important as the evaluation progresses to pointed monitoring and research.

1. Bighorn Sheep Redistribution from Native Range to L&GR.

Description: Bighorn sheep have redistributed from native range to L&GR. Redistribution is asymmetrical with potential and realized productivity and horn classes of rams in the Northern Rockies. Adult sex composition of ~ 50:50, lambs as 16% of total bighorn sheep with ~ 60% of all rams classified as large (Class III & IV) horned is typically reported on L&GR. Bighorn sheep abundance on L&GR varies with season and is inversely related to the periods of greatest biological need. Bighorn sheep presence is highest on L&GR in the fall, reduced in the winter (period of greatest energy and nutrient conservation) and lowest in the summer (period of greatest energy and nutrient acquisition). Productivity of bighorn sheep aggregations on L&GR cannot sustain a population. L&GR is a population sink dependent on emigration from native ranges.

Function: Rams are attracted from a larger area believed to consist of the entire Northern Rockies, but most intensively pulled from the Cadomin and Jasper census zones. Ewes are substantially attracted from the Cadomin and Jasper census zones and within Jasper most intensively from the upper Athabasca River drainage. A change in distribution patterns or increased holdover because of L&GR attraction may contribute to redistribution.

Possibilities: The continual emigration of bighorn sheep from native range will (1) overcome the resiliency of native range productivity causing a decline in the bighorn sheep population in the Northern Rockies; (2) continue to cause a decrease in bighorn sheep abundance in Cadomin and Jasper census zones; (3) be perpetually supported by high native range productivity but decreased abundance to accommodate emigration to L&GR; (4) cease to occur because of deteriorating conditions on L&GR; (5) result in disease spread throughout the Northern Rockies; (6) depress the availability of trophy rams to hunters and; (7) result in harvest restrictions.

2. Bighorns Have Established a Self-sustaining Population on L&GR

Description: Bighorn sheep have established a dense (>20adults/km^2), self-sustaining population on L&GR, characterized by low ewe and lamb presence and high presence of older larger horned rams.

Function: Novel attributes from human modification of the landscape has allowed for some years of immortality, spontaneous generation and lamb ratios highly skewed (>60%) towards ewes, and in spite of the skew required to achieve increased ewe abundance, still achieve a balanced adult sex ratio. High survivorship allows for rapid increase in abundance and density and growth of ram horns

Possibilities: (1) The situation will perpetuate indefinitely because of habitat conditions on L&GR. (2) Maturation and increasing complexity of the ecological system on L&GR will result in predators or intraspecific competition eliminating or suppressing bighorn sheep to densities observed on native range. (3) Bighorn sheep presence and abundance cannot be attributed to immortality, spontaneous generation or skewed sex ratios of lambs.

3. Ram Abundance on L&GR is Characterized by Large Horns

Description: Rams on L&GR are characterized by a disproportionate presence of larger horned animals (~60% class III and IV horn curl), some of which are demonstrated to have relatively large mass (i.e. >180 Boone and Crockett). Ram abundance on L&GR is highest in during the fall hunting season. Hunting is not allowed on L&GR.

Function: Simplified ecological conditions on L&GR may allow rams to use a greater proportion of nutrient intake to grow horns. Decreased rates of harvest may allow rams that occupy L&GR to achieve an older age than those that occupy native range during hunting season. Abundance of large horned rams may result from mature rams immigrating to L&GR with horn mass and length grown in the second and third and possibly 4th year of life that occurred on natal ranges that differ from L&GR.

Possibilities: (1) The perceived decrease in trophy ram availability and the decreased harvest of trophy rams in the Northern Rockies may have occurred because of redistribution of rams to L&GR. (2) Horn mass achieved by bighorns on L&GR may test the capability of (a) a full curl harvest restriction to allow for the availability of trophy rams equivalent to that of a 4/5 curl restriction and (b) protecting younger rams from harvest to contribute to conserving genetic complexity (i.e. approximate a safe operating space).

4. Relocate Bighorn Sheep from L&GR to Maternal Line Natal Native Ranges

Description: Returning bighorn sheep to their source ranges may remove the sink effect pressure on native range productivity. The objective is to restore bighorn sheep abundance on ranges where the productivity occurs, and remove the apparent sink effect and risk of disease spread associated with the observed distribution to L&GR.

Function: This initiative will require identification of genetic population natal range, relocation of ewes and young rams to the maternal line natal range and the active discouragement of bighorn sheep movement to L&GR by physical barrier and behavioural adjustment (e.g. herd dogs). It is unlikely that large older rams can safely be moved to their maternal line native range. One-way gates in the physical barrier will allow for some passive movement to native range.

Possibilities: (1) Bighorn sheep abundances consistent with productivity will be achieved on native range. (2) Risk of disease spread from concentrations of bighorn sheep near L&GR will be reduced. (3) Rams relocated to native range will be with a greater abundance of ewes, increasing ram fertility rates and therefore the opportunity for young rams with fast growing horns to contribute to reproductive output. (4) Return of rams to native range in combination with a full curl harvest restriction will increase ram availability to hunters but protect young rams with fast growing horns from harvest.

5. Genetic Complexity is Fundamental to Population Quality

Description: Genetic complexity is among the processes that enables variation in individual animal response and population tolerance of environmental variation. Wild animals are advantaged by an evolved genetic complexity that benefits resilience and contributes to wild species (1) tolerance of environmental variation, disturbance and regeneration and (2) expands the range of environmental regimes and geographical space that a species may thrive in. Genetic complexity is removed from species that are amenable to domestication

Function: Genetic diversity in wild animals is a function of (1) a complex of genes that govern fitness affecting traits and (2) a diversity of alleles for respective genes within this complex. Allelic presence may vary among populations. Genetic complexity provides tolerance to environmental variations by limiting the individual and population reliance on one or a small number of genes and alleles. Genetic complexity provides safe operating space. Domestication has a profound influence on species. Selection for specific traits and environments reduces genetic complexity and tolerance to environmental variation.

Possibilities: (1) The contribution of distribution processes to population complexity advantages genetic complexity and therefore resilience. (2) Selection pressures from external drivers can be ameliorated by genetic complexity (e.g. hunter selection for trophy horns). (3) Ecological complexity advantages distribution processes and population complexity thereby reinforcing genetic complexity.

6. Bighorn Sheep will Respond to Warming Temperatures and Declining Snow Mass and Depth

Description: Warming temperatures and declining snow mass and coverage increase winter range expanse potentially available for bighorn sheep.

Function: Climate change-caused decreased snowfall and potentially increased melt or sublimation (any of the three variables may account for 0–100% of change) decreases the extent of snow cover and the snowpack depth. This leads to a potential increase for bighorn sheep distribution and occupation.

Possibilities: (1) Ecological and population complexity may be increased, increasing the resilience to winter, improving survivorship including that of new born lambs in the following spring. (2) Bighorn sheep become more widely distributed within current range and may distribute to peripheral range. (3) Bighorn sheep abundance will increase which (a) may be benign, (b) increase opportunities for hunting or other human uses or (c) cause a feedback increasing predation risk because of greater bighorn sheep abundance or apparent competition. (4)The potential for bighorn sheep to occupy landforms previously not used because of snow characteristics increases the potential for heavy snowfall events to trap bighorn sheep groups in low survivability situations for significant time periods. (5) Snow bed duration may be decreased on native range, reducing late summer forage availability and palatability, reducing potentials to acquire nutrients and energy and increasing potentials that landforms with agronomic forage will be used. (6) Icing events become more frequent and severe, increasing bighorn sheep reliance on stored energy and nutrients and therefore summer ranges. (7) Hotspots may be characterized by an increased number of groups, which depending on abundance response may have greater or lesser numbers of individuals in groups.

7. Contribution of Change in Abundance or Distribution to Presence at a Location

Description: The abundance or density of animals at a location is sometimes interpreted as a measure of habitat or population quality. It has long been recognized that abundance alone provides limited information on quality.

Function: The occurrence of animals at a location may occur because of (1) high resource availability enabling productivity and survival, or (2) distribution from other range segments. Distribution may consist of seasonal differences in presence in response to resource or attraction availability. Habitat or population qualities are a function of the demographics and source of animals at a location.

Possibilities: (1) High productivity and survival may perpetuate high abundance providing there are not countering feedbacks including reduced forage abundance and quality, or increased predation or costs to obtain nutrients and energy. (2) Abundance may be inversely related to productivity and survival and be entirely dependent on distribution from other ranges. A high abundance location may be a sink. (iii) A low abundance location may be characterized by high productivity and survival and high distribution and may be a source.

8. Stability is Desirable and the Normal Situation

Description: Resource exploitation commonly desires a consistent supply and rapid recovery from disturbance. Generally bighorn sheep populations tend to have stable abundance, composition and productivity. Productivity is the most volatile of these vital rates.

Function: Perception and relatively short-term exposure to natural environments may have generated the belief that stable states have a narrow range of variation. Management attempts to minimize the variation around equilibrium (e.g. suppression by harvest) can suppress the inherent variability that is advantageous to the species or system. Characteristically stable adult sex rates may accommodate the variability in productivity and survivorship that occur over shorter time periods.

Possibilities: (1) Some vegetation communities in the Northern Rockies may have very narrow ranges of tolerance, and therefore have little resilience to variation. (2)The complexity of the Northern Rockies ecosystems may allow self-organization that advantages from normally occurring variation and is tolerable of periodic novel or extraordinary variation. The complexity and the processes should be the focus of management. (3) Systems and populations are much more variable than perceptions may indicate.

9. Herbivory and Predation Inherently Conflict with Bighorn Sheep Population Quality

Description: Herbivory and predation are fundamental processes that sustain trophic scales and community complexity. Argument has been made that in the absence of management applied external drivers, bighorn sheep depress forage abundance and/or quality resulting in feedback(s) that reduce bighorn sheep productivity, abundance and horn growth rates.

Function: Symbiosis characterizes the herbivore-vegetation relationship. Plants have evolved growth patterns to accommodate grazing patterns and may benefit from nutrient cycling and deposition and seed dispersal by herbivores. Predator and prey relationships are complex and poorly understood. Predators eat prey; a predator is expected to be involved in most deaths or consumption of prey.

Possibilities: (1) An adverse relationship suggests that fundamental processes have been compromised, simplifying trophic relationships and allowing excessive or untimely herbivory or predation. (2) Environmental changes may shift the stable state and restrict vegetation productivity and consequently nutrient and energy available to herbivores. (3) Restricted opportunity to distribute may cause changes in herbivory that vegetation cannot tolerate. (4) Poor habitat quality or skewed age classes may affect the condition of the prey and vulnerability to predation. (5) Prey may be attracted to habitats where topography or resource distribution advantages predators. (6) Environmental changes may increase prey biomass and predator presence (apparent competition). (7) Predation independent of environmental control may be the ultimate cause of death.

10. Scenarios May Cause Timely and appropriate Action

Description: Scenarios are intended to present possibilities. Reconciling human utilization of environments with the persistence of desirable states requires timely and appropriate actions. Desirable state commonly includes persistence of ecological services and biota. Complexity and processes are the essence of managing for desired states and need to be a governance priority.

Function: Scenarios may increase the transparency of human activities and governance that affect the environment. Human utilizations of the environment are implemented consistent with prevailing governance bias and commonly, implementation is characterized as advantageous to the proponent in the immediate time period without adequate regard for broader implications. Transparency is expected to advance the adoption of safe operating space and governance that focuses on complexity and controlling processes.

Possibilities: (1) Scenario presentation of possibilities may allow governance to better define needs and proceed with actions that achieve safe operating space and pointed monitoring or research that improves knowledge and enables appropriate management feedback. (2) The ability to understand the constituents and volatility of complexity and controlling processes will be tested. The potentials and securities required for governance to accommodate environmental and population quality may be better understood. (3) Governance bias may be better revealed and preferably articulated, allowing greater understanding of strengths and weaknesses of governance decisions, allowing management feedbacks.