Elk and Predation in Idaho: Does One Size Fit All?

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Introduction

Predation and predator-prey dynamics are particularly interesting and intriguing aspects of wildlife biology. Though predation is an integral part of population dynamics, the effect of predation on prey populations is less clear, largely because the interaction is complex. For example, the large-ungulate prey base in Idaho includes elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*) and pronghorn (*Antilocapra americana*). The suite of large predators includes black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), wolves (*Canis lupus*), and a few grizzly bears (*Ursus arctos*). Furthermore, the dynamics of individual predator and prey species vary across spatial and temporal scales, as do the interactions among those species.

Changing habitats, management philosophies, and social values also cloud our understanding of predator-prey dynamics (Schwartz et al. 2003). Messier (1991) points out that the emphasis on the limiting effects of predation has likely obscured identification and interpretation of other factors that may ultimately regulate prey populations. Consequently, describing and understanding the effect of predators on prey populations is a significant challenge.

To illustrate this, we have assembled relevant data sets for elk in Idaho. The data were collected as part of several Idaho Department of Fish and Game (IDFG) research efforts aimed at understanding bull-elk mortality, elk recruitment and population processes across large spatial scales. The data are from generally comparable telemetry-based projects with objectives related to survival and cause-specific mortality.

Our objective is to review and discuss these data sets within the context of predator-prey dynamics.

Background

Elk are Idaho's premier big-game animal. The statewide population has increased steadily since the mid-1970s, when hunting for antlerless elk was eliminated throughout most of the state. Idaho elk populations are near all-time highs and are at or near management objectives (Compton 1999). Today, about 125,000 elk are distributed throughout the state from the sagebrush-dominated deserts in southern Idaho to dense, cedar-hemlock forests of the north.

Managing elk populations and their habitats for a sustainable yield is a high priority for management agencies. Habitat-effectiveness models are the primary elk-habitat management tool in the northern Rocky Mountains (Lyon 1979), and harvest is the primary population management tool.

Idaho also supports viable populations of black bears, cougars, coyotes and bobcats. Small populations of grizzly bears occur near the Greater Yellowstone Ecosystem and in the Selkirk and Purcell mountains in northern Idaho. Wolves were reintroduced during 1995 to 1996. The population has grown from 35 to an estimated 512 wolves in 59 packs (Sime and Bangs 2006) distributed across the state.

Approximately 25,000 black bears occur throughout forested habitats in Idaho. Hunter harvest is about 2,000 animals annually, and the populations in most game management unites (GMUs) are considered stable-to-increasing (Nadeau 2005a). Harvest has generally increased since 1994, and management criteria suggest that harvest is "moderate" (Beecham and Rohlman 1994).

Cougars are found throughout Idaho, but they are difficult to monitor because they are secretive, and they occur at low densities. The statewide harvest increased through the late 1990s, peaking in 1997 when 798 animals were reported, then declined to 423 in 2005 (Nadeau 2005b). This suggests that the cougar population has likewise declined over the past decade.

The data sets that we present are derived from localized concern over declining bull-to-cow ratios or poor recruitment and from a general interest in ungulate ecology. Declining bull-to-cow ratios in north and northcentral Idaho in the late 1970s and early 1980s lead to a research effort designed to link elk-population processes with the landscape (Unsworth et al. 1993, Hayes et al. 2002). Hughbanks (1993) conducted a small-scale investigation in southeastern Idaho, and Montgomery (2005) used the combined data to address statewide bull-ecology questions.

Furthermore, concerns related to chronically low or declining calf-to-cow ratios led to two major investigations into the underlying reasons for poor recruitment (Schlegel 1986; Gratson, unpublished report 1992; Zager and White 2003).

More recently, the reintroduction of wolves into Idaho has resulted in renewed interest in broad, ungulate-population ecology and predatory-prey dynamics. In response, the IDFG launched an ambitious research effort in 2005 that includes GMUs (Figure 1) across the state. We provide some preliminary data from that research.

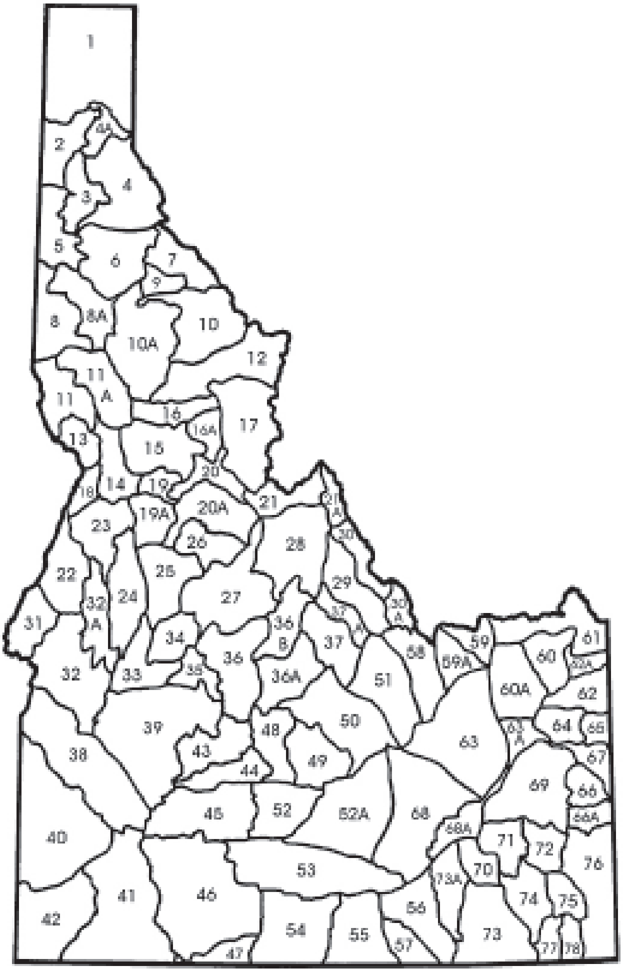
Results and Data Sets

Bulls

Elk-population growth and expansion was uneven across the state. Also, declining bull-to-cow ratios and quality of bulls in the harvest were evident in northern and northcentral Idaho GMUs by the mid-1980s. In response, IDFG launched projects during 1986 to 1995 in 3 in contrasting study areas (Lochsa study area, GMU 12; Coeur d'Alene study area, GMU 4; Sand Creek study area, GMU 60A) to identify the reasons behind this decline.

Across the 3 study areas, bull survival ranged from 0.54 to 0.69, and more than 80 percent of the mortality was related to hunting (Table 1). Therefore, intensive monitoring was limited to just before, during and immediately after the hunting seasons. Mortalities occurring during other seasons were often not promptly investigated, so determining cause of death was problematic. Other causes of death (less than 10 percent of the total mortality) included, but were not

Figure 1. GMUs as delineated by the Idaho Department of Fish and Game.



limited to, predation. Therefore, predation accounted for less than 10 percent of the annual bull elk mortality on these three study areas during this period.

Furthermore, bull survival on the Lochsa study area was modeled using road density, hunter density and an index of topographic roughness as predictive variables (Unsworth et al. 1993). Survival on the Coeur d'Alene study was predicted by total road density and season timing (Hayes et al. 2002). Predation rate was not an important predictor of bull mortality.

However, the reintroduction of wolves during 1995 to 1996 may alter this dynamic. Smith (2005) reported that wolves in Yellowstone National Park prey

Table 1. Adult male elk annual survival rates and cause-specific mortality in Idaho. The time periods are indicated.

					Cause-specific mortality[1]							
GMU	N[2]	Survival	SE	N[2] deaths	Malnutrition disease	Harvest	Other	Bear	Cougar	Wolf	Unknown	Total predation
Panhandle												
GMU 4 (1988–1990)	63	0.549	0.063	28	0	96.4	3.6					
GMU 4 (1991–1994)	128	0.691	0.041	39		92.3	7.7					
Clearwater												
GMU 12 (1986–1990)	169	0.600	0.063	64	0	90.7	9.3					
GMU 12 (1991–1995)	231	0.634	0.065	80		98.8	1.2					
Upper Snake												
GMU 60A (1981–1988)	66	0.543	0.116	40	17.5	80	2.5					

[1] in percent

[2] N indicates mortalities that were investigated; it does not include censored animals.

upon adult bull elk in proportion to their availability. We currently have no data with which to address this question.

Cows

Since 1975, Idaho has managed antlerless elk conservatively, generally resulting in increasing populations and in little interest in data pertaining to survival and to cause-specific mortality of adult female elk. Furthermore, Unsworth et al. (1993) and Leptich et al. (1995) reported adult female elk annual survival rates greater than 0.85 (Table 2). Legal harvest was the primary mortality factor. No predation was documented, but it may have been undetected and reported in the "other" category. Because overall survival was considered adequate, determining mortality factors was a low priority.

More recently, elk populations in several southeastern Idaho GMUs have exceeded management objectives, so harvest goals have been adjusted to reduce the population. The reintroduction of wolves has also created renewed interest in elk population and predator-prey dynamics, and it coincided with IDFG interest in investigating ungulate population dynamics across the range of habitats in Idaho.

Recognizing that ungulate population dynamics likely vary with factors, such as habitat, landscape features, and predator and prey density, multiple study areas were selected to encompass that variability. During the first full year of monitoring (March 2005 to February 2006), preliminary data indicate that adult cow-elk survival ranged from 0.797 to 0.962. Predation (by cougar and wolf) and harvest were the primary proximate mortality factors (Table 2).

Adult-cow survival was less that 80 percent in GMUs 43 and 44, in 10 and 12, and in 60A (Table 2). Coincident with relatively low survival, these populations declined since about 2000 (Compton 2005).

Predation, primarily by wolves, was an important mortality factor in GMUs 43 and 44 (33 percent of the mortality). However, the radio-collared portion of the elk population in GMUs 43 and 44 was concentrated around permanent winter feeding stations, presumably predisposing these animals to predation.

Though predation is the dominant mortality factor for adult cows in GMU 10 and 12, the population decline began in the mid-to-late 1980s, suggesting that factors other than predation initiated the decline.

Body-condition scores (Gerhart et al. 1996; Cook et al. 2001a, 2001b) likely reflect either habitat quality or population density. Because the Lochsa

Table 2. Adult female elk annual survival rates and cause-specific mortality in Idaho. Unless indicated otherwise, the survival period is March 2005-February 2006, cause-specific mortality is derived from March 2005-February 2007.

					Cause-specific mortality[1]							
GMU	N[2]	Survival	SE	N[2] deaths	Malnutrition disease	Harvest[3]	Other[4]	Bear	Cougar	Wolf	Un-known[5]	Total predation
Panhandle												
GMU 4 (1988–1994)	169	0.855	0.018	23		82.5	17.4					0
Clearwater												
GMU 12 (1986–1990)	46	0.886	0.094	5		40	60					0
GMU 10/12 (2005–2006)	44	0.797		25			4		4	80.2	12	96
GMU 15	33	0.878		5					60	40		100
GMU 23	26	0.962		7		42.9	57.1					0
Southwestern Idaho												
GMU 32/32A	29	0.931		7		85.7	14.3					0
GMU 39	27	0.926		6		67			33			33
GMU 43/44	24	0.740		6			33		16.7	33	16.7	67
Salmon												
GMU 28	28	0.893		14	7.1	57.1			28.6	7.1		35.7
GMU 36A	31	0.806		9		44.4			33.3	11.1	11.1	55.6
GMU 36B	31	0.839		14		35.7	14.3		28.6	21.4		50
GMU 50	30	0.833		5		60			40			40
GMU 60A (1981–1988)	53	0.553	0.044	35		74.3	25.7					
GMU 60A (1981–1988)	30	0.733		6	16.7	66.7			16.7			16.7

[1] in percent
[2] N = number of elk years; deaths indicates number of elk that died during the period.
[3] Harvest includes legal harvest, wounding loss and poaching.
[4] Other includes, e.g., vehicle collision, disease ore accident.
[5] Unknown predation includes animals that were killed by a predator, but the species of predator could not be determined with reasonable certainty.

population declined dramatically over the last 20 years, it is more likely that body-condition scores reflect habitat quality in this case.

Body-condition scores for adult female elk were lower in GMUs 10 and 12 than in the other study areas in March 2005 and were lower than GMU 15 in previous sample years pregnancy rates have been variable (Zager and White 2003). If body condition scores reflect habitat quality, it suggests that Lochsa habitats are not as productive as the other study areas, which can result in reduced fecundity, declining recruitment and increased vulnerability to starvation or predation. In fact, Lochsa habitats have changed dramatically during recent decades (U.S. Forest Service 1999). Wildfires in the early 1900s created extensive shrubfields and other early seral habitats used by elk. As these habitats have matured, they became less suitable for elk (Skovlin et al. 2002). Though 96 percent of the mortality is linked to predation, it appears that habitat is contributing indirectly to the elk-population decline in the Lochsa study area.

The elk population in GMU 60A exceeded management objectives. Therefore, the management direction is to increase harvest to bring the population to objective. Lower survival is anticipated and desired under these circumstances.

Cow survival was greater than 80 percent (according to 2005 to 2006 preliminary survival data), and populations were stable-to-increasing since 2000 in the other study areas where recent aerial-survey data are available. Hunter harvest and predation were the primary mortality factors in most of these GMUs. Each of these areas supported viable cougar populations, and wolves were well established by 2000. Predation accounted for approximately 50 percent of the mortality.

Calves

Though elk populations generally increased throughout Idaho after 1975, recruitment remained chronically low in several northcentral Idaho GMUs. Concern over poor recruitment lead to two major investigations into neonatal calf survival and cause-specific mortality in GMUs 10 and 12, the Lochsa study area (Schlegel 1986; Gratson, unpublished report 1992; Zager and White 2003).

During 1973 to 1975, neonatal calf survival from birth to October 1 averaged 37.5 percent. Predation by black bears was the primary proximate cause of mortality (Table 3). In 1976, 75 black bears were removed from the study area. Calf survival increased to 67 percent, then approximated preremoval

Table 3. Survival and cause-specific mortality of elk calves captured and radio-collared as neonates in Idaho. The time periods are indicated.

					Cause-specific mortality[1]							
GMU	N[2]	Survival	SE	N[2] deaths	Malnutrition/ disease	Harvest	Other	Bear	Cougar	Wolf	Un-known	Total predation
Lochsa (1973-1975)	56	37.5		35	2.9	71.4	14.3			11.4		85.7
Lochsa (1976)	18	67		6		83.3				16.7		83.3
Lochsa (1979)	12	25		9		33.3	55.6		11.1			100
Lochsa (1997-2004)	97	0.26		62		54.8	40.3		1.6	3.2		96.7
Lochsa (2000-2004)	57	0.55		21	9.5	38.1	28.6	9.5	9.5	4.8		85.7
South Fork (1996-2004)	102	0.68		30	3.3	40	36.7		10	10		86.7
South Fork (2000-2004)	99	0.39		53	5.7	47.2	26.4		13.2	7.5		86.8
GMU 28 (2006)	34	50			5.9	23.5	11.8	17.6	35.2	5.9		88.1
GMU 36B (2006)	27	52				7.7	15.4	38.5	30.8	7.7		92.4

[1] in percent
[2] N = number of elk years; deaths indicates number of elk that died during the period.
[3] Harvest includes legal harvest, wounding loss and poaching.
[4] Other includes, e.g., vehicle collision, disease ore accident.
[5] Unknown predation includes animals that were killed by a predator, but the species of predator could not be determined with reasonable certainty.

levels 2 years later. Calf-to-cow ratios (an index of recruitment) from aerial surveys showed a similar pattern (Schlegel 1986).

Concurrently, the trend in calf-to-cow ratios was similar in surrounding GMUs, where the bear population was not reduced, compromising interpretation of these results (Schlegel 1986). Nevertheless, these data suggest that predation by black bears is additive and can be a significant factor limiting elk recruitment and population growth.

The second investigation was initiated in 1996, also in GMUs 10 and 12, but north and east of the Schlegel (1986) study. This project was designed to build upon the earlier work (Schlegel 1986) by broadening the scope and addressing some of the criticisms (Gratson, unpublished report 1992; Zager and White 2003).

This investigation contrasted elk population dynamics in a study area with poor recruitment (in the Lochsa study area, GMUs 10 and 12; there were less than 20 calves per 100 cows) and in another with adequate recruitment (South Fork study area, GMU 15; there were more than 30 calves per 100 cows).

Summer (birth to 1 August) calf survival averaged 0.26 on the Lochsa reference area during 1997 to 2004. Predation was the primary proximate cause of mortality. Black bears were implicated in most calf deaths during the first month of life, and cougars were an important mortality factor throughout the remainder of the year (Table 3).

To determine whether predator-caused calf mortality was additive or compensatory, beginning in 2000, black bear and cougar populations were reduced on a 270 square mile (699 km^2) portion of the Lochsa study area. The remainder of the study area served as a reference area where bear and lion populations were not manipulated.

Calf survival increased to an average of 0.55 on the treatment area, but did not change significantly on the reference area. Black bears and mountain lions continued to be the primary proximate mortality factors on both areas (Table 3). Wolves had been well established on the Lochsa study area since about 2000. They are an important source of mortality for older (more than 6-months-old) elk calves but not for younger calves (Tables 3 and 4).

Because few calves radio-collared as neonates survived more than 6 months on the Lochsa, we captured and radio-collared 6-month-old calves in December 2005 and 2006. Comparable data were collected in GMUs 28 and 36B. Among older calves on the Lochsa, wolves were the primary cause of mortality (Table 4).

Table 4. Survival and cause-specific mortality of elk calves captured and radio-collared in December 2005, when they were 6-months-old, through October 2006.

GMU	N[2]	Survival	SE	N[2] deaths	Cause-specific mortality[1] Malnutrition disease	Harvest	Other	Bear	Cougar	Wolf	Un-known	Total predation
GMU 10/12	33	70.0		10			30.0	60.0		10.0	90.0	
GMU 28	36	61.1		14	14.3		42.9	7.1	7.1	28.6	57.1	
GMU 36B	24	58.3		10	10.0		10.0	30.0		50.0	40.0	

On the GMU 15 study area, summer calf survival averaged 0.68 on the reference area during 1997 to 2004. Like the Lochsa study area, predation, mostly by black bears during June and by cougars during the remainder of the year, was the primary proximate mortality factor (Table 3).

To further investigate additive versus compensatory mortality, black bear and cougar populations were allowed to increase (harvest season closed) on a 221-square mile (574 km^2) portion of the area during 2000 to 2004. The remainder of the study area served as a reference.

Calf survival declined significantly on the treatment area, averaging 0.39. Predation, especially by black bears and mountain lions, continued to be the primary proximate mortality factor (Table 3).

Furthermore, White et al. (in prep.) modeled calf survival on both study areas within the context of predator management, landscape and habitat features, and biological factors. Their preliminary models include calf birth weight (index of physical condition) and habitat/landscape features as predictor variables. An index of predator density also contributed significantly to the "best" model for each area (White et al. In Press).

That calf birth weight (index of condition) is an important predictor suggests that neonatal mortality is partly compensatory. That predator density contributes suggests that additive mortality also plays a role.

Discussion

The role of predation in ungulate-population dynamics is unclear, largely because these interactions are complex and difficult to study. Among the wildlife biologists, the traditional view is that most predation is compensatory, i.e., that predators take only those animals that are going to succumb to other factors (e.g., old age, malnutrition, disease) and prey populations respond with increased production and survival. Therefore, predation does not affect prey-population size, but it keeps the population vigorous by removing substandard animals. On the other hand, some recent research suggests that growth rates of prey populations, especially those at low densities, may be limited by predation. In this case, predation is additive because it is in addition to, rather than a substitution for, another form of mortality.

Determining the effect of predators on ungulate populations is difficult because it is a moving target. Predator-prey interactions occur within a matrix of prey species, and several species of predator are distributed across a diverse landscape with changing habitats. Furthermore, the biology of each species is unique and segments (e.g., neonates, juveniles) of populations respond uniquely to the biological setting (Coulson et al. 1997, 1999). In addition, each segment of a population plays a different role in shaping the dynamics of a particular population (Gaillard et al. 1998, 2000).

Evaluating the vital rates (e.g., birth rate, survival rates) of ungulate populations is the best way to assess the effect of predation on an ungulate population. Populations are most sensitive to changes in adult-female survival, followed by reproductive rates of prime-aged adults, age at first reproduction and juvenile survival (Gaillard et al. 1998, Eberhardt 2002).

Cows

We found that adult-female survival was consistently high through time and across the state, and most populations are at or near management objective (Compton 1999). These study areas also support viable populations of black bears, cougars and wolves. Legal harvest and predation were the primary proximate mortality factors. Harvest, assumed to represent additive mortality, was used to reduce cow survival and to maintain those populations within objectives.

Exceptions to this were the Lochsa, GMUs 43 and 44, and the GMU 60A study areas, where survival was less than 80 percent. The elk population in GMUs

43 and 44 is compromised by the presence of permanent winter feeding stations where elk concentrate, presumably making them more vulnerable to predation. The feeding stations were originally established to alleviate excessive winter loss. It is unclear whether they met that objective. Whether survival would improve in the absence of such elk concentrations is also unknown.

The Lochsa elk population decline began in the mid-1980s. Though data establishing cause and effect are not available, this long-term decline may be a result of interactions among factors, including poor or declining habitat; poor or declining calf survival and recruitment; poor adult female body condition; increasing black bear, cougar and wolf populations; and significant mortality associated with the 1996-97 winter. It is not likely that the declining Lochsa elk population is solely a result of predation

The sum of the evidence suggests that inverse density dependence may operate on the Lochsa study area, wherein the elk population has declined to a low level (due to a variety of factors), and predation is maintaining the population at that level. If this is the case, Gasaway (1992) suggested that a regulated predator control may release the ungulate population, and a new predator-prey equilibrium could establish at a higher prey density. The Lochsa study area would provide an interesting test of this hypothesis.

Calves

Our data illustrate the variability in neonatal calf survival across four contrasting study areas. Summer survival was low where the overall population was performing poorly (Lochsa study area). Whereas it was at least 50 percent where populations were stable-to-increasing.

Predation was the primary proximate mortality factor in each area. Bears were important factors in June but not thereafter. Additional data may be required to clarify the relative roles of black bears, cougars and wolves in these areas.

As predicted, summer calf survival increased when bear and cougar populations were reduced on the Lochsa study area and declined when those populations were allowed to increase on the GMU 15 experimental areas. This suggests that calf mortality due to predation was largely additive on these study areas during this investigation. Taken out of context, this implies that predator control is warranted. Though poor calf survival contributes to the Lochsa population decline, addressing adult-female survival should be the first priority (Gaillard et al. 1998, Eberhardt 2002).

Furthermore, advocating predator control is risky. It may be effective over the short term if the ungulate population is below carrying capacity, if predation is additive and if the predator population can be reduced significantly. Generally, increased harvest of predators by sportsmen and sportswomen is not an effective tool for increasing ungulate populations because those efforts are typically spatially and temporally restricted (Stewart et al. 1985). Thus, agency intervention or extreme measures are necessary to reduce predator populations significantly (e.g., Ballard 1991, Boertje et al. 1991, Zager and White 2003). The effectiveness of such measures is temporary and can be costly.

The Future

With the reintroduction of wolves in 1995 to 1996, the predator-prey dynamic in Idaho is in transition, and it may be decades before an equilibrium is achieved (Coulson et al. 2004; White and Garrott 2005a, 2005b). It is unlikely that the data we presented represent that equilibrium because they are limited spatially and temporally. The data should be viewed within the context of larger scale and longer term ecosystem dynamics. Defining and identifying the equilibrium will require long-term research and monitoring of the predator and prey populations, of their habitats and of relevant human influences. For instance, we found little evidence of predation on adult-bull elk in hunted populations. However, these data were collected before wolves were an important component of the community. We expect this dynamic will change because wolves select adult bulls in proportion to their availability in the Greater Yellowstone Ecosystem (Smith 2005).

Furthermore, ecosystems are dynamic, and habitats change as part of the natural process. The dynamics of predator and prey populations undoubtedly change concurrently (e.g. Schwartz and Franzmann 1991), even without human intervention. This argues for using the historical range of variability (Morgan et al. 1994) within an ecosystem as a starting point for conservation and management activities. Such an approach will provide a more reasonable framework for decision making and for temper expectations.

Research Needs

Important questions need to be answered before we can fully understand the effect of predation on ungulates. The first step is to clearly differentiate between the fact of predation and the effect of predation. Further, if we are to advance our understanding, research should focus on pertinent concepts such as ultimate versus proximate factors, compensatory versus additive mortality, density dependence versus density independence versus inverse density dependence, and predation rates.

Significant recent research in Alaska (e.g., Gasaway et al. 1992, Keech et al. 2000, Bertram and Vivion 2002) has provided important insights and offers a sound basis for developing hypotheses and appropriate experimental designs. Additional work in other ecosystems will also provide important insights.

This research will be difficult because understanding predation is expensive and time consuming. Furthermore, some fundamental management and research tools are missing. It is difficult to estimate ungulate population size and even more difficult to estimate predator numbers. Population estimates form the backbone of population dynamics research. Inaccurate or imprecise population estimates hamper interpretation of the data and may lead to incorrect conclusions.

The universal nature of the questions, the difficult logistics, and expense of such investigations argue for an adaptive management approach (Walters 1986) and collaboration across jurisdictions. This approach can be used to test hypotheses and experimentally investigate important questions and, if conducted thoughtfully and properly, will bridge the gap between research and management.

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