The role of American black bears and brown bears as predators on ungulates in North America

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Abstract: American black bears (*Ursus americanus*) and brown bears (*U. arctos*) can be important predators on neonatal ungulates. They prey less commonly on adult ungulates. Bear predation appears to be additive at low ungulate densities and may become compensatory as prey density approaches carrying capacity, *K*. As such, black and brown bear predation can limit, but generally does not regulate, ungulate populations. Maternal and neonatal physical condition, birth synchrony, and birth mass may predispose neonates to predation or other mortality factors. Though black and brown bear predation is an important proximate cause of ungulate neonatal mortality, habitat quality and quantity are important ultimate factors influencing this dynamic. Manipulating bear populations to enhance ungulate populations may be successful in the short-term if predation is additive, but long-term success has not been demonstrated.

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 (Ballard et al. 2001). This is especially so for American black bear (*Ursus americanus*) and brown or grizzly bear (*U. arctos*, hereafter brown bear) predation on ungulates. Such predation has been shown to be an important proximate cause of ungulate, especially neonatal, mortality in North America, but the effect on prey populations is murky, for several reasons. Black and brown bears are opportunistic omnivores, rather than obligate carnivores, that respond to a wide variety of locally available food sources that are often seasonal. As such, bear predation on ungulates varies widely in response to geographic, seasonal, and spatial factors. Bears often function in a multi-predator system, further complicating interpretation of their role. Changing habitats, management philosophies, and social values (Schwartz et al. 2003) also cloud our understanding of predator–prey dynamics. 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.

Our objective is to review and discuss the role of black and brown bears as predators on ungulates in North America within a context of proximate versus ultimate factors and to offer a broad-scale approach to address some persistent questions.

Definitions

Misuse of terminology such as limiting and regulating factors, compensatory and additive mortality, and density dependent and density independent factors has limited our understanding of predator–prey relationships (Messier 1991, Sinclair 1991, Skogland 1991, Boutin 1992, Dale et al. 1994). In this paper, we define these terms as follows.

A limiting factor is anything that reduces the rate of population growth. It may be density dependent, density independent, or inversely density dependent. A regulating factor maintains a population in approximate equilibrium by affecting long-term natality and mortality rates. Such an equilibrium depends on density dependent factors. Therefore, regulating factors (density dependent factors) are a subset of limiting factors. Furthermore, all mortality factors are limiting, but only density dependent factors are regulating (Messier 1991, Sinclair 1991).

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Density dependent factors affect natality and mortality rates in proportion to population density. For example, a high-density population is likely to have a relatively low natality rate and a relatively high mortality rate, whereas a low-density population is likely to exhibit relatively high natality and low mortality rates (Caughley and Sinclair 1994). Density independent factors are unrelated to population density; for example, weather may affect birth and death randomly rather than in proportion to population density (Caughley and Sinclair 1994).

If predation, for example, acts as an inversely density dependent factor (depensatory effect), then it is destabilizing because predators would kill a decreasing proportion of the prey population as it increases. More important for conservation purposes, if a prey population declines, predation acting in an inversely density dependent manner would take an increasing proportion of the prey and exacerbate the decline (Caughley and Sinclair 1994). Mortality is considered additive when that animal would have otherwise lived to reproduce. Mortality is considered compensatory when that animal would likely have died due to other causes before reproducing (Gasaway et al. 1992).

Bears as opportunistic predators

Because bears are omnivorous and typically have access to a wide range of foods, a very loose predator–prey relationship results (Ballard and Larsen 1987). The nature of this relationship makes it particularly difficult to determine the effect of predation by bears on ungulate populations. Black and brown bears were considered minor predators until the mid-1900s. Although animal remains were commonly reported from food habit analyses, they were generally interpreted as a result of scavenging activity (Seton 1929, Chatelain 1950, Jonkel 1978). More recently, black and brown bears have been implicated as effective predators on ungulates (Schlegel 1976, Franzmann and Schwartz 1986, Larsen et al. 1989, Ballard 1992). However, the role bears play as predators on ungulates apparently varies considerably. Even though black bears have been identified as important predators on ungulates, studies on black bear diets in the Great Smoky Mountains (Beeman and Pelton 1980), Alaska (Hatler 1972), Idaho (Beecham and Rohlman 1994), Montana (Tisch 1959), western Washington (Poelker and Harwell 1973), and Banff National Park (Raine and Kansas 1990) did not identify ungulate neonates as a major food source.

Black and brown bears can be characterized as opportunistic predators (Herrero 1978). When ungulate prey is spatially and temporally available, predation may provide a significant proportion of their energy and nutrition (Reynolds and Garner 1987, Boertje et al. 1988), especially before green-up when other foods are less available (Adams et al. 1995). Ballard et al. (1981) demonstrated that predation declined as alternate foods became more available, resulting in a lower impact on a moose (*Alces alces*) population.

Predation on ungulates is apparently a learned behavior. Observations of brown bears in Yellowstone National Park (French and French 1990) and black bear scat analysis on the Kenai Peninsula (Schwartz and Franzmann 1991) indicate that the feeding habits of individual bears within a population occur along a gradient from highly predatory to little or no predatory activity. Some authors reported that adult males were more predatory than other age and sex classes (Boertje et al. 1988, Gunther and Renkin 1990, Jacoby et al. 1999), although others (Ballard et al. 1981, Reynolds and Garner 1987) found no significant difference in the predatory behavior of male and female bears.

By definition, bears limit ungulate populations. But because they are opportunistic predators and their role as a predator varies with the availability of prey, alternate foods, and habitat quality, it is unlikely that bears play a strong regulatory role in most ungulate populations (Van Ballenberghe and Ballard 1994).

Predation on ungulates

Before the widespread use of radiotelemetry, bears were considered scavengers rather than predators (Jonkel 1978). More recently, several studies on ungulate predation in North America demonstrated that black and brown bears can be important predators of neonatal elk (*Cervus elaphus*; Schlegel 1976, Smith and Anderson 1996, Singer et al. 1997, Zager and White 2003), moose (Franzmann et al. 1980, Schwartz and Franzmann 1991, Ballard 1992, Ballard and Van Ballenberghe 1997), deer (*Odocoileus* spp.; Ozoga 1982, Wilton 1983, Kunkel and Mech 1994), and caribou (*Rangifer tarandus*; Miller and Broughton 1974; Bergerud 1980; Miller et al. 1988; Mahoney et al. 1990; Siep 1991, 1992).

Black and brown bears also prey on adult moose, elk, and caribou in the western US and Canada (Ballard 1992). Brown bears were the primary cause of mortality among adult female moose in several studies in Alaska and Canada (Larsen et al. 1989, Ballard et al. 1991, Keech et al. 2000, Bertram and Vivion 2002). However, annual survival of adult females often remained high ($\geq$90%) from year to year and population to population,

regardless of the dominant mortality factors. This suggests that predation on adults generally had an inconsequential effect on the overall population trajectory, because eliminating predation would have had relatively little effect on survival of adult females (Modafferi and Becker 1997; Gaillard et al. 1998, 2000). However, Boertje et al. (1988) reported that adult male brown bears killed 3.3–3.9 adult moose annually and females without cubs killed 0.6–0.8 adult moose and 0.9–1.0 adult caribou annually in east central Alaska. Predation at this level can affect the ungulate population trajectory, especially in relatively low-density ungulate populations (Boertje et al. 1988). Based on food habits and observations, Gau et al. (2002) reported that barren ground brown bears on their central Canadian arctic study area were effective predators on caribou throughout the active season. Haglund (1974) reported that brown bear predation on adult moose in Sweden was localized and sporadic. Danilov (1983) suggested that brown bears were more important predators on adult moose in northern than in southern systems.

In reviews of elk and moose calf mortality in North America, researchers reported that predation by black or brown bears was consistently the most important source of mortality (Schlegel 1976, Ballard 1992, Smith and Anderson 1996, Ballard and Van Ballenberghe 1997, Singer et al. 1997, Zager and White 2003). Investigations focusing on radiocollared neonatal ungulates showed that predators accounted for >90% (range = 56–100% for moose; 44–98% for elk) of neonate deaths (Table 1 and 2), and that survival during the first 2–4 months of life can be <10% (Franzmann et al. 1980; Ballard et al. 1981, 1991; Larsen et al. 1989; Osborne et al. 1991; Gasaway et al. 1992; Zager and White 2003). Losses during the remainder of the year were fewer (survival at 8 weeks = 0.49 and 0.56 vs. annual survival = 0.26 and 0.40 on 2 north central Idaho study areas; Table 2), but still contributed to low annual survival rates (Van Ballenberge 1987, Zager and White 2003).

The predatory role of black and brown bears appeared to be positively related, but not directly proportional, to their relative densities (Ballard et al. 1990, Schwartz and Franzmann 1991). Ballard (1992) and Ballard and Van Ballenberghe (1997) reported that moose calf mortality rates ranged from 2.7 to 52.2%, with lower rates associated with relatively low brown bear densities (12 bears/1,000 km^2; Table 1). Mortality rates from black bear predation studies ranged from 2 to 50% when bear densities were 16–570 bears/1,000 km^2. Black bears were a significant cause of calf moose mortality when they occurred at relatively high densities of >200 bears/1,000 km^2 (Table 1; Ballard 1992).

Ballard (1992) reported that in studies where predation from brown bears was considered the most important cause of mortality, investigators considered such mortality as additive. Brown bear and moose densities in these studies ranged from 10 to 28 bears/1,000 km^2 and from 175 to 9,000 moose/1,000 km^2, respectively. In studies where black bears were the largest cause of moose mortality, both bear and moose densities were high (200–570 bears/1,000 km^2 and 500–3,700 moose/ 1,000 km^2, respectively). On the Kenai Peninsula, Alaska, where black bear density was nearly 10 times greater than that of brown bears and moose densities ranged from 1,000 to 3,700 moose/1,000 km^2, predation by black bears was probably a compensatory form of mortality because a moderate number of calves survived through autumn only to die of starvation during winter (Schwartz and Franzmann 1991). However, in Saskatchewan, where moose densities were lower (450 moose/ 1,000 km^2), predation by black bears was probably an additive form of mortality because annual calf survival increased short term following reductions in bear densities (Stewart et al. 1985).

In north-central Idaho in the mid-late 1970s, 58% of 86 Rocky Mountain elk calves radiocollared shortly after birth and monitored until 1 October died from natural causes (Schlegel 1986). Of these, 98% died due to predation and 2% as a result of disease. Predation by black bears accounted for 66% of the total mortality by predators (Table 2). Average annual mortality of radiocollared elk calves in eastern Washington was 53% (Myers et al. 1998, Table 2). Predation was the proximate mortality factor in nearly 78% of the deaths. Nearly 49% of the deaths were attributed to mountain lions (Puma concolor), and black bears were implicated in 15.9% of the mortalities.

Smith and Anderson (1996, 1998) reported a 15% mortality rate for 164 radiocollared elk calves monitored through 15 July in the Jackson Hole and Grand Teton National Park areas. Of the mortality, 58% was due to predation, primarily by black bears (Table 2). Predation was disproportionately higher on male calves and those born earlier in the calving season. Summer herd composition surveys showed that higher calf:cow ratios were associated with higher April precipitation levels.

Annual elk calf mortality was 57% in Yellowstone National Park (Coughenour and Singer 1996, Singer et al. 1997, Table 2). They reported that 32% (n = 127) of radiomarked calves died during summer and 21% died during winter. Nearly all summer mortality (n = 39) was

Table 1. Causes of mortality and survival rates of radiocollared moose calves to November in relation to observed predation rates and predator densities in North America (modified from Ballard 1992, Ballard and Van Ballenberghe 1997).

	Southcentral Alaska				Kenai Peninsula, Alaska		Southwest Yukon[a]	East interior Alaska[a]	West interior Alaska[a]	Gasaway[a]	East central Alaska	Saskatchewan	New Brunswick	Newfoundland
	Areas 1–3	Area 1	Area 4	Pooled areas	1947 burn	1969 burn								
Years	1977, 1978	1979	1984	1977–84	1977, 1978	1981, 1982	1983, 1985	1998–2000	1988–90	1981–88	1984	1982	1983, 1985	1983, 1988
Number of calves	124	28	46	198	47	74	117	62	89	33	33	12	11	88
Mortality (%) caused by														
grizzly bear	41.9	42.9	52.2	44.0	34.0	6.4	3.4	19	2	52	2.7	41.9	51.5	
black bear			8.7	2.0		35.1		21	38	3	3.0	50.0	9.1	30.0
grizzly and black bears						2.7								
wolf	1.6		6.5	2.5	6.4	1.4	17.9	1	11	15	15.2			
unknown predation	2.4			1.5	4.3	2.7	2.6	3						
miscellaneous	4.8	14.3	13.1	8.1		5.5	6.0	4	16	12	12.1			
unknown	3.2		2.2	2.5	1.3	1.4	9.4	33						
Survival, %	46.0	42.9	17.4	39.4	44.6	48.5	18.8	16	18–21	32	18.2	50.0	81.8	70.0
Density, per 100 miles^2 (per 100 km^2)														
moose	168.4 (65)	181.3 (70)	231 (89.2)	168.4 (65)	259 (100)	958.3 (370)	57 (22)	120–180		88–157	45.3 (17.5)	116.6 (45)		777 (300)
grizzly bear	6.2 (2.4)	2.6 (1.0)	7.3 (2.8)	6.2–7.3 (2.4–2.8)	3.1–7.3 (1.2–2.8)	3.1–7.3 (1.2–2.8)	4.1 (1.6)	10		16	4.1 (1.6)	0	0	0
black bear	0	0	23.3 (9.0)	0–23.3 (0–9.0)	53.1 (20.5)	66.8 (25.8)	4.1 (1.6)[c]	86–265			2.1–2.8 (0.8–1.1)	51.8–103.6 (20–40)	Mod?[b]	147.6 (57)
wolf	0.47–0.93 (0.18–0.36)	0.59 (0.23)	0.72 (0.28)	0.47–0.93 (0.18–0.36)	2.85 (1.1)	2.85 (1.1)	1.1 (0.41)[d]	4		2.2–5.4	1.0 (0.40)	Low?[b]	0?[f]	0
Calf moose kill rate by														
grizzly bear				0.097	0.019[e]	0.103[e]	0.085[e]				0.143			
black bear														
Daily adult moose kill rate by														
grizzly bear			0.025	0.023			0.022							
Sources[f]	1	2	3	3, 4	10, 12	9, 12	11	16	17	18	7, 8, 15	5, 13	6	14

[a] Causes of mortality and survival rates are annual estimates.

[b] Question mark indicates an estimate based on professional judgment. Mod. = moderate.

[c] Black bear densities not estimated but thought to be similar to grizzly bear densities (D.G. Larsen, personal communication as cited in Ballard 1992, Ballard and Van Ballenberghe 1997).

[d] Average late winter density for 1983 and 1985.

[e] Assumed all mortalities occurred between birth and mid-July, i.e. 60-day period. Derived by dividing estimated number of calves killed by 60 days.

[f] 1 = Ballard et al. (1982), 2 = Ballard and Miller (1990), 3 = Ballard et al. (1990), 4 = Ballard et al. (1991), 5 = Beaulieu (1984), 6 = Boer (1988), 7 = Boertje et al. (1987), 8 = Boertje et al. (1988), 9 = Franzmann and Schwartz (1986), 10 = Franzmann et al. (1980), 11 = Larsen et al. (1989), 12 = Schwartz and Franzmann (1991), 13 = Stewart et al. (1985), 14 = Mercer (personal communication as cited in Ballard 1992, Ballard and Van Ballenberghe 1997), 15 = Boertje (personal communication as cited in Ballard 1992, Ballard and Van Ballenberghe 1997), 16 = Bertram and Vivion (2002), 17 = Osborne et al. (1991), 18 = Gasaway et al. (1992).

Table 2. Elk calf survival rates and cause-specific mortality factors reported from Washington, Wyoming, and Idaho, 1973–2003.

	Blue Mountains, Washington[a]	Jackson Hole, Wyoming[b]	Yellowstone National Park[c]	Lochsa 1973–1979[d]	Lochsa 1997–2003[e]	South Fork, Clearwater River[e]
Survival rate						
annual	0.47	0.58	0.43	—	0.26	0.40
SE	0.032	0.002	0.179	—	0.043	0.048
summer	—	0.84	—	0.420	0.49	0.56
SE	—	0.001	—	0.048	0.049	0.048
n[f]	240	164	127	105	106	107
Annual cause-specific mortality						
grizzly bear	—	—	16.9	—	—	—
black bear	15.9	50.0[i]	1.5	66.0	40.6	36.4
unknown bear	—	—	4.6	—	—	—
cougar	48.6	—	1.5	20.0	38.7	35.5
coyotes	4.7	18.2	16.9	—	—	0.9
bobcat	—	—	—	2.0		0.9
wolf	—	—	—	—	0.9	—
eagle	—	—	1.5	—	—	—
unknown predation	8.4	—	1.5	10.0	6.6	12.1
total predation[g]	77.6	68.2	44.4	98.0	86.8	85.8
Other[h,i]	22.4	31.8	55.2	2.0	13.2	13.9

[a]Myers et al. (1998).
[b]Smith and Anderson (1998). Summer time frame is birth through 15 Jul.
[c]Singer et al. (1997).
[d]Schlegel (1986). Summer time frame is birth through 1 Oct.
[e]Zager and White (2003). Summer time frame is birth through 1 Aug.
[f]Number of radiocollared elk calves.
[g]Proportion of calf mortalities that were due to predation.
[h]Includes 1 mortality likely caused by black bears.
[i]Includes disease, accident, human caused, and unknown causes.

due to predation by brown bears (28% of the mortality), black bears (3%), and coyotes (*Canis latrans*; 28%), whereas winter mortality ($n = 26$) was mostly associated with malnutrition during the severe winter of 1988–89, following the drought and extensive wildfires of 1988. Singer et al. (1997) suggested that summer calf mortality was partially compensatory in this high density elk population. This dynamic will likely change with the re-introduction of gray wolves (*Canis lupus*) into the Yellowstone Ecosystem and concurrent 50% reduction in the northern range elk population (White and Garrott 2005*a*, 2005*b*).

Predation has been identified as an important source of caribou calf mortality (Miller and Broughton 1974, Bergerud 1980). The mortality pattern was similar to that of moose and elk wherein most caribou neonate deaths occurred within the first month of life (Bergerud 1971, 1980; Miller and Broughton 1974; Miller 1987; Mahoney et al. 1990; Whitten et al. 1992; Adams et al. 1995), after which they became less vulnerable to bear predation with increasing age and mobility (Adams et al. 1995).

Predation on neonatal ungulates is closely related to spring weather patterns and its influence on forage distribution. Snow-free habitats prevail during an 'early spring' and ungulates are typically widespread, making them less vulnerable to predation. During a 'late spring,' green-up is delayed and spatially restricted due to slowly receding snow. Ungulates tend to concentrate in the relatively snow-free areas, making them more vulnerable to predation (Bergerud 1971).

Habitat structure may also be important. Predation rates on elk calves doubled (29% vs. 13%) after the 1988 wildfires in Yellowstone National Park (Singer et al. 1997). They suggested that reduced shrub cover made calves more vulnerable to predation.

Bear population response

The availability of meat influences habitat quality for black and brown bears at the individual and population level (Reynolds and Garner 1987, Schwartz and Franzmann 1991, Hilderbrand et al. 1999). Stringham

Table 3. Population parameters for black bear and brown bear populations in Alaska with varying levels of neonatal ungulate use.

	Kenai Peninsula 1947 burn[a]	Kenai Peninsula 1969 burn[a]	Western Brooks Range[b,c] (*n*)	Canning River[b] (*n*)	Arctic National Wildlife Refuge[b,d] (*n*)
Bears/1000 km²					
black	205[e]	265[e]	—	—	—
brown	—	—	2.28	0.68	1.59
Calf predation					
moose calves eaten/bear > 1 yr old	1.4[e]	5.3[e]	—	—	—
Caribou calves preyed upon?	—	—	yes	no	yes
Age at first litter	5.8[e]	4.6[e]	7.6 (16)	9.7 (19)	7.3 (16)
Reproductive interval	2.2	2.1	4.1 (16)	—	4.1 (20)
Average litter size	2.2	2.3	1.95 (44)	1.85 (20)	2.05 (40)
Cub survival	0.74[e]	0.91[e]	—	—	—

[a]Schwartz and Franzmann (1991).
[b]Reynolds and Garner (1987).
[c]In the Western Brooks Range, 13 of 13 kills observed from 25 May through 25 Jun were calves.
[d]In the Arctic National Wildlife Refuge, 14 of 15 kills observed from 25 May through 10 Jul were calves.
[e]Pairs of values in same row significantly different at $P = 0.05$.

(1990) suggested that the reproductive rate is positively related to body size among North American brown bears. Hilderbrand et al. (1999) showed that the proportion of salmon (*Oncorhynchus* spp.) in the diet is significantly correlated with adult female body size, litter size, and population density.

However, it is doubtful that neonatal ungulates play a role comparable to that of salmon. Salmon may comprise >50% of the diet during late summer and autumn when coastal bears are growing and accumulating fat reserves (Hilderbrand et al. 1999). Neonatal ungulates are far less concentrated and abundant than salmon. Furthermore, they are typically available for about 4 weeks in spring when bears are replenishing lean body mass, rather than growing (Hilderbrand et al. 1999).

Schwartz and Franzmann (1989, 1991) linked black bear population productivity on the Kenai Peninsula to the availability of moose calves which, in turn, was linked to habitat productivity following wildfire. Age at first reproduction, interval between weaning yearlings, cub survival, and body size were significantly better for black bears that occurred in an area with high versus low moose density (Table 3). At a proximate scale, Schwartz and Franzmann (1989, 1991) attributed the bear population response to the availability of moose calves. Ultimately, however, both the moose and black bear population were likely responding to the high quality, early successional habitat resulting from a wildfire in 1969 versus more mature, less productive habitat in the 1947 burn area.

Reynolds and Garner (1987) found that brown bear populations with access to caribou calving areas oc-

curred at higher densities than those without such access (Table 3). Furthermore, the higher density populations were more productive. Three-cub litters were relatively common in the high density populations, but none were observed in the lower density population. However, they did not address possible confounding factors such as differences in overall habitat productivity or food habits, compromising interpretation of these findings.

Bear population manipulations

The perception that bears are a universally significant predator on ungulate populations has led to *de facto* bear reduction programs in Alaska; Quebec, Canada; and the western US. Although reduction programs may seem justified in the most simplistic sense, they ignore the complexity of the predator–prey dynamic.

A number of investigators have examined the impact of bear population reduction on ungulates with mixed results (Schlegel 1976, Stewart et al. 1985, Ballard and Larsen 1987, Crête and Jolicoeur 1987, Ballard and Miller 1990, Ballard et al. 1991, Miller and Ballard 1992). Black bear predation on a relatively low-density elk population in Idaho appeared to be additive (Schlegel 1986). Elk survival and recruitment increased for 2 years following removal of 75 black bears from a north central Idaho study area. Recruitment (the proportion of calves surviving to 1 year) declined to pre-removal levels after 2 years (Table 4). This interpretation is compromised, however, by a similar, albeit less dramatic, pattern observed in nearby drainages

where the bear population was not manipulated. The increasing elk population also coincided with a shift from liberal either-sex elk hunting to a more conservative bulls-only season (Schlegel 1986).

Several others (Beasom 1974, Stout 1982, Stewart et al. 1985) showed significant increases in offspring ratios following control. Investigations in south-central Alaska (Ballard et al. 1991), east-central Alaska (Boertje et al. 1988, Gasaway et al. 1992), and southwestern Yukon (Larsen et al. 1989) described moose populations well below what they assumed the habitat could support and where predation was largely or totally additive. After reviewing several North American studies, Ballard (1992) concluded that bear predation on neonates became increasingly additive as moose density declined from about 700 to 175 moose/1,000 km^2.

In a higher density elk population in the Yellowstone National Park area, bear predation appeared to be at least partially compensatory because about 20% of the calves that survived to autumn succumbed to winter malnutrition (Singer et al. 1997).

Bear predation can have a disproportionately greater impact on low- versus high-density moose populations (Gasaway et al. 1992). Bear predation is, therefore, capable of limiting moose (and presumably, ungulates in general) populations at low densities for extended periods, as exemplified by the low density dynamic equilibrium (Gasaway et al. 1992). Most evidence suggests that neonatal ungulate mortality from predation through autumn is additive; it also appears that predation becomes more compensatory at higher versus lower ungulate density (McCullough 1979, 1984). When ungulate populations approach or exceed carrying capacity, K, reductions in predator populations will likely have little effect on ungulate population growth because such mortality is probably compensatory (McCullough 1979, 1984; Crête 1987; Gasaway et al. 1992). Conversely, when prey populations are well below K and limited by predation, mortality can be reduced significantly when predator populations are reduced.

Therefore, habitat changes that result in increasing ungulate density or K may reduce the effect of predation on ungulate neonates and, therefore, the perceived need to manipulate predator populations. However, if the ungulate population has declined to very low levels as a result of poor habitat, excessive adult female mortality rates (due to hunting), or severe weather, predators may take an increasing proportion of the prey population, resulting in a further decline. In such instances, predation is inversely density dependent, and prey may find themselves in a predator pit (Smuts 1978, Krebs

Table 4. Selected elk calf parameters before (1973–75) and after (1977–79) removal of 75 black bears from a north central Idaho study area (Schlegel 1986).

	Pre-bear removal			Post-bear removal		
	1973	**1974**	**1975**	**1977**	**1978**	**1979**
Calf survival (%)[a]	56	33	35	67		25
n[b]	9	24	23	18		12
Bear-caused mortality (%)[c]	75	56.3	86.7	83.3		33
n	3	9	13	5		3
calf:100 cow ratio		28	13	61	51	27

[a]Percent of radiocollared calves captured as neonates and surviving to 1 Oct.
[b]Number of radiocollared calves monitored.
[c]Proportion of calf mortality caused by black bears.

1996). Escaping a predator pit may take decades or active management. It is unlikely that habitat improvements will result in a significant response in the short-term under these circumstances (Gasaway et al. 1992).

In each case, it appears that bear population reductions by translocation or increased harvest resulted in short-term, but not long-term, increases in ungulate calf survival. However, the results are often equivocal, making interpretation difficult because studies were often observational or lacked a robust and appropriate experimental design. Furthermore, there was no clarification of the interactive effects of predation, factors predisposing calves to predation, and other mortality factors that may have limited the ungulate populations (Boutin 1992). Nevertheless, the body of work addressing this issue is strongly suggestive and should not be ignored.

There does not appear to a strong regulatory feedback mechanism in the interaction between bear and ungulate populations. Though most authors consider predation by bears to be density-independent, bear population manipulations will affect prey populations differently, depending on prey density in relation to K. As such, predation by bears functions as a limiting factor, but does not regulate most ungulate prey populations.

Predisposition of prey

Most mortality among ungulates, regardless of cause, occurs during the first few weeks of life. This corresponds to the time during which neonatal ungulates are most vulnerable to predation by bears. Bear-caused mortalities decline thereafter, presumably because offspring become less vulnerable with increasing age and mobility (Bergerud 1971, 1980; Miller and Broughton

Table 5. Physical condition of adult female elk; mass at birth and annual survival of elk calves in the Lochsa River and South Fork of the Clearwater River drainages, north central Idaho, 1997, 1998, and 2004.

Area	Year	Adult female elk			Male calf birth		Female calf birth		Annual calf		
		BCS[a]	SD	n	Mass (kg)[b]	SD	Mass (kg)[b]	SD	Survival[c]	SD	n
Lochsa	1997	6.1	1.92	17	14.1	3.45	13.0	2.85	0.06	0.06	27
	2004	8.9	1.72	24	18.3	3.33	16.3	2.27	0.51	0.09	24
South Fork	1997	8.9	1.16	18	14.1	3.33	15.1	3.31	0.56	0.14	31
	1998	9.8	1.2	13	16.9	2.31	16	2.88	0.43	0.33	28
	2004	9.9	1.95	7	16.3	4.97	19	4.23	0.52	0.14	30

[a]Body condition score after Gerhart et al. (1996).
[b]Age after Johnson (1951) and estimated birth weight after Smith et al. (1997).
[c]Survival estimates after Pollock et al. (1989).

1974; Ballard et al. 1981; Miller 1987; Boertje et al. 1988; Larsen et al. 1989; Mahoney et al. 1990; Whitten et al. 1992; Kunkel and Mech 1994; Adams et al. 1995). However, neonatal ungulates may be predisposed to predation by poor body condition, weather, habitat, disease, or other influences. If this is the case, bear predation on ungulates would be compensatory, rather than additive (Boutin 1992).

Testa et al. (2000) found a significant relationship between moose calf age (during the first 65 days) and the likelihood of survival. They found that early-born calves had better survival than late-born calves and that the age-specific mortality during the first 65 days declined from 0.04/day to nearly 0. Furthermore, moose calf survival through July was 0.27 (SE = 0.03), whereas the annual rate was 0.22 (SE = 0.03). Therefore, most moose calf mortality evidently occurred during the first 2 months of life. Brown bears were the primary mortality factor.

Early and synchronous parturition is an advantage among North American ungulates (Estes 1976; Whitten et al. 1992; Adams et al. 1995; Smith and Anderson 1996, 1998; Singer et al. 1997; Gregg et al. 2001, Testa 2002). Testa (2002) posits that early-born calves achieve needed size and mobility before predators can adjust to the seasonal availability of vulnerable prey. As predator search image changes, ungulate parturition is at a peak, and the predator population is swamped. Late-born calves become especially vulnerable because there are fewer calves for the predators that have belatedly adjusted to the availability of neonatal ungulates.

Noyes et al. (1997) demonstrated that bull elk age structure influences the timing and length of the rut and, by extension, the timing and length of the calving period. When breeding activity was dominated by mature (>2 years old) bulls, the rut was earlier and significantly shorter, resulting in a more synchronous calving period. They reconfirmed the role of male age

structure, but cautioned that the nutritional condition of the females is also an important piece of this puzzle (Noyes et al. 2002).

Neonatal survival is positively correlated with birth mass for red deer (*C. elaphus*), elk, white-tailed deer, caribou, and pronghorn (*Antilocapra americana*) whether or not predation is significant (Verme 1965, 1969; Thorne et al. 1976; Guinness et al. 1978; Clutton-Brock et al. 1982; Fairbanks 1993; Oldemeyer et al. 1993; Kunkel and Mech 1994; Adams et al. 1995; Singer et al. 1997). Birth mass may be affected by population density (Gaillard et al. 1998) and maternal condition which, in turn, are strongly influenced by habitat and weather. Females in poor condition as a result of inadequate habitat or severe winter weather produce offspring with low birth mass that are born later than those of females in good condition (Verme 1977, Adams et al. 1995, Singer et al. 1997, Testa and Adams 1998, Keech et al. 2000, Cook et al. 2004). Survival declines for such low birth mass and late born offspring (Singer et al. 1997). In north central Idaho, elk in relatively poor condition following a severe winter (1997) produced calves that were 3.3–4.3 kg lighter than after an average winter (Table 5).

In a lower elevation study area (South Fork), where the 1997 winter was less severe than Lochsa, cows were in better condition but calf birth mass was still 2.2–3.9 kg lower than after a more normal winter (Table 5). Interpreting changes in annual survival was compromised by an experimental manipulation of black bear and mountain lion populations in the intervening years.

Blood and serum parameters have been used to index animal condition (Seal et al. 1978; DelGiudice et al. 1990, 1994). Kunkel and Mech (1994) reported that serum urea nitrogen was the only factor that differed significantly between surviving and perishing white-tailed deer (*O. virginianus*) fawns (Table 6), but the importance of this was not clear. Zager and White

(2003) found no significant differences in blood parameters (Table 6) or birth weights of elk calves that succumbed to predation and those that did not. Ballard et al. (1996) found no apparent measurable effect on neonate moose blood parameters or weights following a severe winter (Table 6).

Maternal age structure may also influence neonatal survival. Mature white-tailed deer exhibit more effective maternal behavior than younger females, and mature females are markedly more successful in the presence of predators (Ozoga and Verme 1986). But Guinness et al. (1978), working in an environment devoid of large predators, found that that birth mass was more important than maternal experience in determining neonatal survival.

The relationships among habitat quality and quantity, maternal condition, timing of parturition, birth mass, and offspring survival suggest that habitat plays a subtle but important role in shaping predator–prey dynamics. Though predation is the most obvious proximate cause of mortality in these systems, habitat provides the ultimate framework within which these processes function.

Discussion

The general perception amongst the public and many biologists is that predators regulate large mammal populations (Keith 1974). Although it is clear that black bears and brown bears prey on ungulates, their role in ungulate population dynamics is less certain. In some systems, brown bears are an important cause of adult female ungulate mortality. However, overall survival often remains >90% (as long as hunting is not an issue), so the ungulate population remains stable. In most cases, adult female survival among large herbivores is consistently high, regardless of the dominant natural mortality factors (Gaillard et al. 1998, 2000).

More commonly, black bears and brown bears prey upon neonatal ungulates <1 month old, taking up to 90% of the offspring annually. Survival of pre-weaned juveniles often varies in time and space and, as such, can have important effects on prey population dynamics, especially at low prey population levels (Gaillard et al. 1998, 2000).

Unfortunately, the literature inadvertently paints a biased picture. Most of the research that focuses on ungulate population dynamics, including recruitment, is undertaken to address a perceived problem. Research reports on populations where calf survival is strong, recruitment meets objectives, and the overall population is self-sustaining are the exception in wildlife literature.

Taken out of context, this implies that predator control is the order of the day. Predation, by definition, is a limiting factor in these communities. Not all ungulate populations are declining, even where they are sympatric with 1 or more species of predator. A review of bear food habits indicates that for many bears or bear populations neonatal ungulates are not important food items. Furthermore, neonatal survival is not a significant management issue in many ungulate populations.

Nevertheless, identification of bears as important predators on neonatal ungulates has created a dilemma for wildlife managers in the western US, Alaska, and Canada. Taking a simplistic approach, many publics demand predator control to maximize ungulate populations regardless of the effect on the prey population. This often results in liberalized hunting of predators or other steps to reduce their influence. The response is directed at addressing a proximate factor influencing the ungulate population, but ignores other factors that may ultimately limit ungulate population growth or recovery.

Emphasizing increased harvest and predator management may be effective short term if the ungulate population is below K, predation is functioning as an

Table 6. Blood and serum parameters evaluated from neonatal white-tailed deer, moose, and elk.

Parameter	White-tailed deer[a]	Moose[b]	Elk[c]
Serum urea nitrogen	X[d]		
Creatinine	X		X
Thyroxine (T4)	X		
Triiodothyronine (T3)	X		
Packed cell volume		X	
Hemoglobin		X	
Calcium		X	X
Phosphorus		X	X
Glucose		X	
Total protein		X	X
Albumin		X	
Betaglobulin		X	
Selenium			X
Zinc			X
Iron			X
Magnesium			X
Copper			X
Triglycerides			X
Cholesterol			X
Sodium			X
Potassium			X

[a]Kunkel and Mech (1994).
[b]Ballard et al. (1996).
[c]Zager and White (2003).
[d]Significantly different between neonates that lived and those that died.

additive mortality factor, and the predator population can be reduced significantly. Generally, increased bear harvest by sportsmen has not been 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. Moreover, the emphasis on predator reduction often obscures identification and interpretation of other factors that ultimately regulate prey populations (Messier 1991). Ultimately, predator reduction programs reduce the effectiveness and damage the credibility of management agencies.

We argue that managers may be attempting to respond to public pressure to fix something that isn't necessarily broken. It should not be assumed that maximizing the ungulate population is 'natural' or represents a 'balanced' system. Common sense argues against a management program wherein the ungulate population (or any other component) is maximized. Gasaway et al. (1992) suggested that low-density moose populations were the norm in areas where predators were lightly harvested, even during pristine times. There is no reason to assume such systems, under similar circumstances, should function differently today.

It should not be assumed that the current snapshot of an ecosystem represents conditions over the long term. Nor should it be assumed that a 50-year-old snapshot is a good representation. Ecosystems are dynamic and habitats change dramatically as part of a natural progression of events, such as wildfire and plant succession. The dynamics of resident predator and prey populations undoubtedly change concurrently with these ecosystems (Schwartz and Franzmann 1991).

This concept argues for parameterization of the historical range of variability (Morgan et al. 1994) within an ecosystem and then using that as a starting point for conservation and management plans. Once the historical range of variability is framed, human influences such as timber harvest and road building must be superimposed because they also dramatically alter plant communities and ungulate productivity and mortality rates.

Identifying and defining the changes that have occurred in communities, and the reasons behind those changes, offers a better chance of understanding the ultimate factors that influence predator–prey dynamics. Once that understanding is achieved, it is important that all stakeholders participate in a cooperative effort to develop a conservation plan in which goals (population,

habitat, ecosystem) and strategies are developed and clearly presented (Gasaway et al. 1992, Bertram and Vivion 2002). This can be a challenge where the public believes that maximizing the prey (ungulate) population should be the primary goal.

Nevertheless, such conservation plans should be framed around the concept of change and the historical range of variability. Because our understanding of predator–prey systems is imperfect, an adaptive management (Walters 1986) approach wherein different predator and prey management strategies are employed within an experimental framework and the results are carefully monitored could be implemented effectively. An adaptive management approach is also appealing because wildlife managers cannot wait for the results of long-term research projects to provide insights.

Research needs

Until relatively recently, studies focused on the fact of predation rather than the effect of predation and the ultimate factors that drive these systems. This shift in research emphasis to investigate the factors that might drive these systems is important and should continue. Some of the more recent studies (Gasaway et al. 1992, Keech et al. 2000, Bertram and Vivion 2002) provide important insights and offer a sound basis for developing hypotheses and appropriate experimental designs.

Many questions remain regarding bear predation on ungulates (Linnell et al. 1995, Ballard and Van Ballenberghe 1998), including ultimate versus proximate factors; compensatory versus additive mortality; density dependence versus density independence versus inverse density dependence; and predation rates. Most research on bear predation has occurred in northern systems and where bears were part of a multi-predator system. Investigations in other ecosystems will provide important insight.

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 (but see Samuel et al. 1987, Miller et al. 1997). 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 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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