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Author(s): Bruce L. Smith

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Invited Paper:

WINTER FEEDING OF ELK IN WESTERN NORTH AMERICA

BRUCE L. SMITH,¹ National Elk Refuge, P.O. Box 510, Jackson, WY 83001, USA

Abstract: Winter feeding of elk (*Cervus elaphus*) is a topic that has engendered a great deal of debate among wildlife biologists, policy makers, and the general public. The first institutional feeding of elk in North America occurred in Jackson Hole, Wyoming, where several thousand elk are still fed during most winters at the National Elk Refuge. Winter feeding of elk is employed on an annual basis by state agencies in Idaho, Oregon, Utah, Washington, and Wyoming. During 1995–99, an average 31,000 elk were fed in those 5 states at a cost of \$1.6 million. Most feeding programs originated due to conflicts between elk and agricultural uses of historic elk winter range. Wildlife managers generally resorted to feeding to reduce damage by elk to crops, and to provide economic benefits of maintaining more elk than diminished winter habitat could sustain. Several negative consequences result from feeding elk. These include (1) the monetary costs of feeding, which divert dollars from other resource programs; (2) excessive herbivory that alters plant community structure and consequently affects the value of habitats near elk feedgrounds to other wildlife species; (3) changes in elk behavior that are of both spatial and philosophical significance; (4) diseases, which are more readily transmitted among densely concentrated animals, threaten the welfare of elk and other species, and shape resource management; and (5) public perceptions that may lead to the devaluing of habitat. These consequences argue for a shift from a production–consumption model of elk management toward management that embraces conservation of all species, maintenance of ecosystem functions, and sustainability of resources. I suggest proactive alternatives to winter feeding, which may avert conflict situations that precipitate public and political pressures to feed elk.

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Key words: agriculture, *Cervus elaphus*, economics, elk, disease, feeding, feedground, growth, habitat, management, population.

Winter feeding of elk occurs at a number of locations in western North America. Elk feedgrounds are small, but because of the migratory nature of most elk herds, landscape-scale impacts of feeding programs are possible. The objectives of this paper are to explore the purposes, advantages, and liabilities of feeding; to review the geographic distribution of elk feeding; and to detail the effects of feeding at the individual, population, and community levels. Because winter feeding is the exception to the system by which most elk herds are managed, a perspective of the origin of feeding to mitigate wildlife–human conflicts is instructive.

Bunnell (1995) reported that nearly 1 million elk inhabited North America in 1995—a remarkable recovery from the 50,000 reportedly remaining at the turn of the 20th century (Seton 1927). This restoration of elk is attributed to a legacy of conservation including: regulation of hunting; law enforcement; the reservation of wildlands in national forests, national parks, national wildlife refuges, and Bureau of Land Management lands;

research elucidating the ecological requirements of elk; and habitat improvement programs of state and federal agencies and conservation organizations. In 1 dramatic instance, early efforts to recover elk to presettlement numbers were also aided by the initiation of winter feeding.

Of the 50,000 elk left in North America at the century's end, most were found in the remote lands in and around Yellowstone National Park (Seton 1927). At the southernmost extent of this refugium lay Jackson Hole, 1 of the last intermountain valleys in the United States settled by people of European descent. Here the conflicts between settlers, their livestock, and elk reached epic proportions between 1890 and 1910, focusing a nation's attention on the plight of wildlife as civilization advanced westward (Anderson 1958, Wilbrecht and Robbins 1979). Elsewhere, elk either had retreated from the advance of western settlement, or simply were eliminated by hunting for sport and market. But most importantly, competition between elk and livestock for common resources—winter food and habitat—all but doomed the vast herds of elk, bison (*Bison bison*), pronghorn (*Antilocapra americanus*), bighorns (*Ovis canadensis*),

¹ E-mail: bruce_smith@fws.gov

and other big game. Their disappearance from many places either went unnoticed or was considered a necessary passage in the taming and civilizing of the American West (Hornaday 1931, Trefethen 1961).

Yet as elk vanished from most of their range, the combination of Wyoming's grand venue and the growing prospect of local extinction evoked a conservation imperative that overcame the ardor of humans for the taming of wildlands and their wild inhabitants. The story of the people and politics that rescued the Jackson Hole elk has been eloquently recounted (Leek 1909, Preble 1911, Graves and Nelson 1919, Betts 1978). In short, the recommendations of E. A. Preble and D. C. Nowlin (Preble 1911), scientist of the Bureau of Biological Survey and Wyoming game warden, respectively, were largely implemented. The 1911 "Preble Report" advocated the reservation of a permanent winter range in Jackson Hole as "essential for the proper protection of the elk. Such a refuge should be of considerable size, should be situated in a valley which the elk naturally seek, and should comprise pasturelands, as well as meadows which will produce hay for feeding the animals after they have exhausted the available forage."

During 1912, the United States government purchased about 800 ha of private lands adjacent to the town of Jackson as a nucleus of the National Elk Refuge (NER). With a legislative appropriation of \$5,000 in 1910, the state of Wyoming had already begun the practice of winter feeding. During 1911, the state passed a memorial entreating the U.S. Congress to financially assist with the feeding of the Jackson Hole elk. Congress complied with an appropriation of \$20,000 to investigate the situation, to begin trapping and removal of elk from Jackson Hole, and to purchase hay. Thus began the first government-subsidized feeding of wildlife.

The 1872 establishment and early protection of Yellowstone National Park by the U.S. cavalry, which predated the beginnings of the NER by 40 years, was an equally bold conservation move. In Yellowstone, too, winter feeding was previously conducted to enhance survival of elk and bison, albeit on a less extensive scale than in Jackson Hole (Houston 1982). In addition to winter feeding, several thousand elk were trapped and translocated by truck and train from the NER and Yellowstone to reduce those populations. These elk restocked depleted ranges throughout North America (Robbins et al. 1982).

DISTRIBUTION OF FEEDING PROGRAMS

A telephone survey of wildlife agencies in the western states and provinces provided information on winter feeding of elk (Table 1). Since the establishment of the NER, the state of Wyoming has established 22 additional elk feedgrounds west of the Continental Divide during the 1950s–80s. Elsewhere in North America, winter feeding of elk is a rarity. Only in Idaho, Oregon, Utah, and Washington are public herds of elk annually fed (Table 1). About 23,000 elk are fed during winter in Wyoming and 8,000 are fed in the other 4 states (Table 1). Thus, only 3% of the estimated 1 million elk in North America are fed by management agencies during winter.

These data represent elk feeding programs that occur on an annual or nearly annual basis (depending largely on weather conditions). Not included is feeding that occurs on an emergency basis to avert high mortality of animals during extreme weather conditions, or to mitigate a specific elk damage problem on a nonrecurring basis. For example, Colorado has fed elk during severe winters, and the Colorado Division of Wildlife has developed a priori criteria that guide decision-making regarding when feeding should be initiated. Alberta does not feed elk on an annual basis, but uses "intercept feeding" to deter elk in specific situations from feeding on or damaging crops, primarily haystacks.

Moreover, in most western states and provinces, private citizens feed free-ranging elk, either deliberately or unintentionally. Deliberate feeding may be motivated to enhance wildlife viewing or to improve elk survival. Most winter feeding by citizens is purely incidental to the feeding of livestock, and the elk are either tolerated or unwanted on livestock feedlines. It would be difficult to quantify the numbers of elk that occasionally or even regularly consume hay intended for livestock, forage grain crops, or browse fruit trees. Such numbers may be substantial during severe winters. The information I present pertains only to winter feeding programs for elk that are sanctioned by state or federal agencies. In most situations, agencies conduct all program phases, from purchase or production of the hay to its distribution to the elk. In some cases, public funds are used to purchase hay, but private citizens do the feeding.

Throughout this paper, the elk feeding programs in Wyoming, and the NER in particular, are highlighted. Those programs account for

Table 1. Distribution of winter feeding of elk in North America. The number of elk fed and number of days of feeding are based on averages for 1995–99. Figures are based on 1994–98 for Utah and Wyoming.

State	Location (herd)	Land jurisdiction ^a	No. of elk fed	No. days of feeding	Type of hay fed	Reasons for feeding ^b
Idaho	Donnley	Pvt	100	140	Baled	2
Idaho	Stanley (≤17 sites)	USFS, Pvt	240	<80	Pelleted	4
Idaho	Sun Valley–S. Fork Boise River (6 sites)	USFS	925		Pelleted	1, 7
Idaho	Swan Valley (3 sites)	USFS, Pvt	740		Baled	2, 5
Idaho	Total		2,005			
Oregon	Elkhorn (10 sites)	State, Pvt, BLM	1,400	145	Baled	2, 3
Oregon	Wenaha	State	523	70	Baled	2
Oregon	White River	State	350	90	Baled	2
Oregon	Jewel Meadows ^c	State	275	90	Baled	2, 4, 6
Oregon	Total		2,548			
Utah	Hardware Ranch	State	490	93	Baled	2, 4
Washington	Yakima (13 sites)		3,000	80–100	Baled	2
Wyoming	National Elk Refuge	USF&WS	9,200	65	Pelleted	1, 2, 3, 7
Wyoming	Alkalai (Jackson)	USFS	663	99	Baled	2
Wyoming	Fish Creek (Jackson)	USFS	827	101	Baled	2
Wyoming	Patrol Cabin (Jackson)	State	442	90	Baled	2
Wyoming	Camp Creek (Fall Creek)	State	628	97	Baled	2
Wyoming	Dog Creek (Fall Creek)	USFS, Pvt	712	113	Baled	2
Wyoming	Horse Creek (Fall Creek)	State	1,137	99	Baled	2
Wyoming	South Park (Fall Creek)	State	1,150	120	Baled	2
Wyoming	Dell (Hoback)	USFS	232	138	Baled	2
Wyoming	McNeel (Hoback)	Pvt	512	135	Baled	2
Wyoming	Grey's River (Afton)	State	956	129	Baled	2
Wyoming	Forest Park (Afton)	USFS	810	133	Baled	3, 7
Wyoming	Jewett (Piney)	State	612	153	Baled	2
Wyoming	Finnegan (Piney)	BLM	386	160	Baled	2
Wyoming	Franz (Piney)	BLM	426	154	Baled	2
Wyoming	North Piney (Piney)	BLM	305	136	Baled	2
Wyoming	Bench Corral (Piney)	State	566	80	Baled	2
Wyoming	Black Butte (Green River)	State	555	148	Baled	2
Wyoming	Green River Lakes (Green River)	USFS	468	104	Baled	3, 7
Wyoming	Soda Lake (Green River)	State	785	79	Baled	2
Wyoming	Fall Creek (Pinedale)	State, BLM	776	126	Baled	2
Wyoming	Scab Creek (Pinedale)	BLM	566	164	Baled	2
Wyoming	Muddy (Pinedale)	USFS	677	145	Baled	2
Wyoming	Total		23,391			

^a BLM = Bureau of Land Management, Pvt = private, USFS = U.S. Forest Service, USF&WS = U.S. Fish and Wildlife Service.

^b The following reasons for feeding elk were identified by state wildlife managers: (1) loss of winter range to residential development, (2) conflicts on adjacent agricultural lands/to alleviate wildlife damage, (3) to increase elk numbers for hunting, (4) to provide public viewing of elk and related economic benefits, (5) elk migrations to winter range are short-stopped by livestock operations, (6) to make trapping and removal easier, and (7) public concerns about winter mortality of elk.

^c Roosevelt elk are fed at this location.

75% of the elk fed on the continent each winter, and they are the longest running, best documented, and best known of the elk feeding programs. Furthermore, the Wyoming situation is singular due to widespread brucellosis infection of elk in the western part of the state.

EFFECTS OF WINTER FEEDING ON ELK POPULATIONS AND PHYSIOLOGY

Studies of survival, reproduction, and physical development of winter-fed elk have been conducted in northwest Wyoming and Utah. These

studies were designed in part to reveal individual and population-level responses to winter food supplementation.

Physical Development

Body mass of winter-fed elk from Utah and Wyoming is similar to that reported for other Rocky Mountain elk (*C. elaphus nelsoni*; Dean et al. 1976, Thorne and Butler 1976, Taber et al. 1982). Elk and red deer typically lose body mass in winter, which they regain during the growing season (Mitchell et al. 1976, Nelson and Legee 1982). When supplementally fed, elk may lose, maintain, or gain body mass in relation to the ration provided. Adult females maintained in pastures with limited natural forage at the NER lost 10.8%, 6.2%, and 4.2% of body mass from late January to early April on rations of 0.95, 1.03, and 1.36 kg of pelleted alfalfa/100 kg of body mass, respectively (Oldemeyer et al. 1993). Changes in body mass of female elk held in paddocks during winter and fed 1.7 kg of hay/100 kg body mass varied from -9.5% when fed baled hay to -4.2% when fed pelleted hay (Thorne and Butler 1976). At Utah's Hardware Ranch, a ration of 3.2 kg of meadow hay (approx. 1.4 kg/100 kg body mass) allowed adult females to maintain body mass during winter (Kimball and Wolfe 1984). Bailey (1999) found no difference in body condition between supplementally fed elk and free-ranging elk in the Jackson herd during 2 winters, based on body fat indices and allantoin:creatinine ratios.

Winter feeding may be expected to improve antler growth of elk by retarding loss of body mass during winter and necessary recovery during the period of antler growth (Kozak et al. 1994). Antler mass achieved by elk at the NER was similar to that reported in unfed elk herds (Flook 1970, Wolfe 1983, McCorquodale 1989). Antler mass of 2- to 15-year-old elk that died during 1989-94 on the

NER was unrelated to the amount of feed those elk received, and the number of days they were fed during the winter prior to growing their last set of antlers. Instead, early growing season temperatures during March and April of the spring preceding their deaths, and ambient temperatures when male elk were in utero (which also correlated with cohort birth mass) were correlated with antler size (Smith 1997). The former effect emphasizes the sensitivity of antler growth to prevailing foraging conditions during each year of life (Taber 1959, Bubenik 1982). The latter provides additional evidence that environmental conditions during the birth year influence growth, reproductive success, and survival of cervids (Albon et al. 1987, Mech et al. 1991).

Reproduction

With elk, body mass attained by fall can influence conception rates (Sadlier 1969, Mitchell et al. 1976). However, there is no evidence that body mass differs between fed and unfed elk herds. Likewise, pregnancy rates of adult elk (≥ 2 -year-old) (87% at NER, 85% at Hardware Ranch) and yearling elk (17% at NER, 12% at Hardware Ranch) fed during winter (Kimball and Wolfe 1979, Smith and Robbins 1994) are similar to those reported in other elk populations (Houston 1982, Taber et al. 1982).

Although supplemental feeding has elevated fecundity of white-tailed deer (*Odocoileus virginianus*; Ozoga 1987), the same has not been shown for elk. In western Wyoming, midwinter calf:cow ratios are lower than in adjacent states and east of the Continental Divide in Wyoming, where elk are not fed during winter. Since 1982, the numbers of elk in the Jackson herd and the number wintering on the NER have increased (Fig. 1). This resulted from low winter mortality and the difficulty of achieving desired harvests of elk, particularly those that spend summer in national parks (Boyce 1989, Smith and Robbins 1994, Smith and Anderson 1998). However, midwinter calf:cow ratios have declined, and are inversely correlated with elk numbers on the NER (Fig. 2). Moreover, summer recruitment of calves since 1990 in Grand Teton National Park, where half of NER elk spend summer, is inversely correlated with elk counted from helicopter in the park's central valley (Fig. 2).

Bailey (1999) found no difference in fetal growth between supplementally fed elk and free-ranging elk of the Jackson herd. At the rates and duration that supplemental feeding occurs at the NER, winter feeding did not produce larger birth

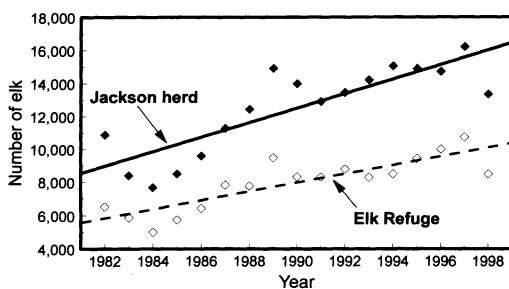


Fig. 1. The number of elk counted in the Jackson herd and on the National Elk Refuge during winters 1982-98.

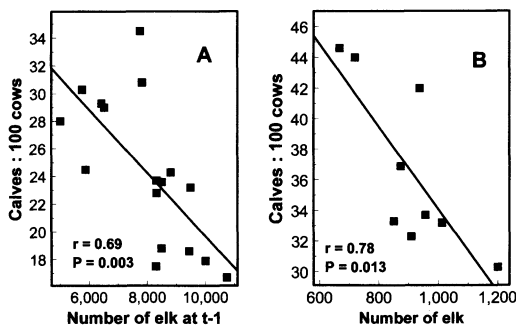


Fig. 2. Calf:100 cow ratios at the National Elk Refuge during winters 1983–99 regressed on number of elk counted on the National Elk Refuge the previous winters (A), and calf:100 cow ratios in Grand Teton National Park regressed on number of elk counted during summers 1991–99 (B).

mass than reported for elk that are not fed (Smith et al. 1997). As in red deer, cohort birth mass varied with annual spring temperatures and consequent growth of new grass during their birth year (Albon et al. 1987). This is not surprising because most fetal growth occurs during the last 2 months of gestation (Nelson and Legee 1982), after winter feeding has ceased at the NER.

There was evidence that winter feeding influenced sex ratios at birth. More males were born after winters when feeding began earlier and the digestibility of the feed was higher (Smith et al. 1996). Survival of male fetuses, which are energetically more costly to produce than females (Clutton-Brock et al. 1982), may be favored by nutritional supplementation early during gestation.

Survival

Winter mortality was reported to regulate red deer on the Isle of Rhum, Scotland (Clutton-Brock et al. 1985), and elk in northern Yellowstone National Park (Houston 1982, Singer et al. 1997) in a density-dependent fashion. Winter feeding can reduce mortality of elk during severe winters or on overstocked ranges. Winter mortality of elk on western Wyoming feedgrounds averages <1.5% annually (Boyce 1989; J. Bohne, Wyoming Game and Fish Department, personal communication). Annual mortality of elk at Utah's Hardware Ranch is <1% (Lou Cornicelli, Utah Division of Wildlife Resources, personal communication). Wildlife managers in the other states where elk are fed report similarly low mortality on feedgrounds.

Radiocollared calves of the Jackson elk herd that were supplementally fed on the NER had higher winter survival (0.886; $P < 0.04$) than calves

that were not fed (0.714). However, survival of calves on the NER declined as the number of days the elk were fed during winter increased (Smith and Anderson 1998). Elk were fed longer during protracted winters. Thus, feeding cannot negate environmental stressors completely, and maintaining elk on feedgrounds for protracted periods may increase the risk of mortality from disease (Smith and Roffe 1994, Smith and Anderson 1998).

RATIONALES FOR FEEDING

The desire to maintain larger numbers of elk than available winter habitat can sustain is generally at the root of feeding programs. In most situations, winter habitat has been fragmented, degraded, or usurped by land uses such as ranching, farming, subdivisions, or road construction. Conflicts between elk and human uses of the land have ensued.

Among the western states and provinces, feeding of elk is far more prevalent now than prior to 1950. Winter feeding of elk was generally initiated in response to political pressure and remains popular with the public. The following reasons are cited by wildlife managers for feeding elk in winter: (1) Feeding can maintain a larger number of elk than remaining habitat can support, enhancing hunting opportunities. (2) Feeding can make elk more available for public viewing, and commercial benefits can result. (3) Feeding may reduce winter mortality of elk and assuage public concerns about animal welfare. (4) Feeding alters winter distribution of elk, helping to keep elk off private lands where damage to crops, orchards, and fences occurs, and off roadways where motorist safety may be of concern.

BENEFITS OF FEEDING ELK DURING WINTER

Economic and Recreational Opportunities

Feeding elk during winter engenders recreational opportunities for harvest, viewing, and photography of elk. Feeding also enhances economic opportunities for guiding and outfitting, and related businesses that benefit from consumptive and nonconsumptive uses of wildlife. In Wyoming, where state law does not permit nonresident hunters to hunt big game without a guide in any of the 15 national forest wilderness areas within the state, the outfitting business benefits from elk feedgrounds. The more elk that are available, the more hunting licenses are available. As more licenses become available, opportunity to outfit elk hunts increases. During 1980, the

outfitting business in Teton County, Wyoming, generated \$2.4 million in direct sales from hunting of big game animals (Taylor et al. 1981). Not all of this was related to elk hunting, of course. However, community businesses realize indirect revenue from both resident and nonresident elk hunters purchasing outdoor equipment, food, lodging, and entertainment. Applying a multiplier to account for indirect revenue, the outfitting business generated \$4.2 million in economic activity in Teton County (Taylor et al. 1981). Expenditures related to elk hunting occur during fall when local economies may experience a lull between summer and winter tourist seasons.

Private contractors offer horse-drawn sleigh rides through feedgrounds at the NER, Donnelly, Idaho, and Hardware Ranch, Utah. Prices charged for rides in 1999 ranged from \$3.50/adult at Hardware Ranch to \$12.00/adult at the NER. These private business endeavors can provide opportunities for public education. State personnel escort the public to view and help feed elk at Jewel Meadows in Oregon.

Mitigation of Human–Wildlife Conflicts

Controlling distributions of elk provides safety, economic, and public relations benefits. Feeding elk may improve transportation safety by short-stopping elk that would cross roads and highways during spring and fall migrations to reach more distant winter ranges than locations where feedgrounds are established.

Many states and provinces have legislated wildlife depredation laws. Winter feeding has been promoted to reduce compensation payments to landowners. Elk that might otherwise migrate through or winter on private lands and consume or damage crops are attracted or hazed to feedgrounds that are generally located on public lands. To further limit elk access to private lands, 65 km of 2.5-m-tall drift fences have been built in western Wyoming to funnel elk to the Grey's River, Soda Lake, and Muddy Creek feedgrounds. Eighty km of fence prevent elk from reaching wheat and hay crops at White River, Oregon, where 7,000 deer and 350 elk are fed. Near Yakima, Washington, over 160 km of elk-proof fence prevent elk from straying into fruit orchards. Decision-makers in those states believe it is cheaper to fence and intentionally feed elk than it is to compensate landowners for damaged crops.

Additional benefits accrue from discouraging elk from using private lands, particularly in states with compensation laws or in states that harbor elk carrying brucellosis. Efforts to limit access of elk to

private lands may conciliate landowners, legislators, and local communities. Should transmission of brucellosis from elk to cattle occur, the potential economic hardships have been amply detailed (Thorne and Herriges 1992, Thorne et al. 1996, Kreeger et al. 2001). During 1992, a Wyoming rancher sued the federal government and the state of Wyoming in separate court actions alleging that wild elk or bison infected his beef cattle with brucellosis (Keiter and Froelicher 1993, Carlman 1994). Although both federal and state judges did not find for the plaintiff, hard feelings and criticism of wildlife managers ensued. Costs of elk management increased as state officials intensified efforts to haze elk from private lands, and conducted depredation hunts of elk during midwinter.

Additionally, during 1997, the state of Wyoming asked the U.S. Department of Agriculture (USDA) to review the state's brucellosis program. Wyoming requested the review to ensure the state's competitiveness in interstate livestock commerce. Wyoming accepted the USDA recommendations, including the testing of cattle in 6 western counties for brucellosis. All 44,000 head of cattle tested during 1998 were found to be disease-free (Dr. James Logan, Wyoming state veterinarian, letter dated 15 March 1999, to the Wyoming Livestock Board). Nonetheless, efforts to eliminate brucellosis in elk and wild bison, and to prevent brucellosis transmission to cattle, have escalated in Wyoming and the adjacent states of Idaho and Montana (Thorne and Herriges 1992, Kreeger et al. 2001).

COSTS OF FEEDING ELK

Economic

The financial requirements to feed elk during winter are both capital and recurring. The NER program has evolved from feeding loose hay from horse-drawn sleds to a fully mechanized operation that distributes processed feed. The changes came as a result of the loss of traditional hay supplies in northwest Wyoming, and escalating labor costs (Robbins et al. 1982). A 1974 memorandum of understanding between the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service calls for a maximum of 7,500 elk to be maintained on the NER each winter. The capital costs required to annually feed this number of elk include 4 >1,000-ton-capacity feed storage sheds, 3 Caterpillar crawler tractors and wagons, 1 Osh Gosh articulated feedtruck, a feed off-loading beltveyor, 4 forklift vehicles with 1-ton-capacity buckets for loading feed into trailers, and a good mechanic.

Table 2. Cost of feeding 7,500 elk for an average 79 days/winter (the past 25-year average) on the National Elk Refuge, Wyoming, in 1999 dollars.

Item	Cost/day	Cost/winter
Pelleted alfalfa (28 tons/day)	4,060	320,740
Labor	180	14,220
Fuel	32	2,528
Total	4,272	337,488

The direct, recurring costs include contracting and purchase of about 2,400 tons of pelleted alfalfa, salaries of feedtruck drivers, and fuel. Indirect costs include contracting, administrative, maintenance, and biological monitoring support, and equipment depreciation. The annual recurring cost of just distributing feed to 7,500 elk averages \$337,488 (Table 2). The U.S. Fish and Wildlife Service and Wyoming Game and Fish Department split the cost of the pelleted alfalfa fed on the NER. The U.S. Fish and Wildlife Service pays all other costs.

I contacted wildlife managers in those states with ongoing elk feeding programs to ascertain feeding costs. Feeding 1 elk for 1 winter ranges from \$35 to \$112 (Table 3). These costs do not include administration, contracting, or biological monitoring of feeding programs.

Idaho—The Idaho Fish and Game Department feeds elk from 3 herds in the western and central part of the state. In addition, there are 3 locations in eastern Idaho, collectively referred to as Swan Valley, where the state has purchased hay that private citizens or state employees fed elk in recent years. Since 1984, when annual feeding of elk was initiated in Idaho, the total cost of feeding has been \$2,400,000. Idaho spent \$133,000 during 1998, exclusive of permanent employee salaries, to feed elk. A similar amount was spent to feed just the Sun Valley–South Boise River elk during winter 1996–97.

Oregon—Wildlife officials began feeding elk in Oregon in 1953 at the Wenaha Wildlife Management Area. Both Rocky Mountain and Roosevelt (*C. elaphus roosevelti*) elk are now fed at 4 locations across the state. The feeding program currently costs the Oregon Department of Fish and Wildlife \$158,500 annually.

Utah—Feeding began at Utah's Hardware Ranch in 1947 to prevent elk from following traditional migration routes down the Cache Valley, where depredations on orchards and agricultural fields were occurring. During the 1980s, Kimball and Wolfe (1984) reported an annual cost to feed

500 elk of \$75,000, or \$150/elk. Estimated annual costs to feed 490 elk at Hardware Ranch during 1995–99 were \$45,000. The higher, former costs arise from the inclusion of permanent salaries associated with administration, contracting, and monitoring. Thus, when all support costs and permanent salaries are included, true costs of feeding elk in Utah and elsewhere significantly exceed the direct costs of provisioning hay to an elk herd.

Washington—This state pays an average \$117,500 annually to feed 3,000 out of an estimated 14,000 elk in the Yakima herd. The program began during the early 1950s in an effort to keep elk from damaging fruit orchards. During the severe winter of 1996–97, elk broke through a 160-km-long "elk-proof" fence in localized areas where they were not being fed. The elk moved onto private lands and caused extensive agricultural damage.

Wyoming—This state estimates that its annual costs to feed about 14,000 elk, plus pay for half of the pelleted alfalfa fed on the NER, approach \$1,250,000 annually. Costs to the U.S. Fish and Wildlife Service average another \$175,000. Additional program costs resulting from the artificial concentration and feeding of elk are management efforts to control and mitigate brucellosis. These programs cost Wyoming another \$250,000 annually.

Thus, the feeding programs in Wyoming are the largest in terms of numbers of elk fed and the state and federal budgets required to sustain the programs. The costs of elk management, including administering feeding operations, biological monitoring, and disease mitigation and research, surpass the income the Wyoming Game and Fish Department derives from the statewide sale of elk licenses. The revenue generated from sale of elk licenses in 1998 was \$7,770,000, but costs of elk management were \$8,820,000. Costs of elk management west of Wyoming's Continental Divide, where the state and federal feedgrounds are located, totaled \$2,758,000 in 1998 compared to license revenues of \$1,846,000 (H. Harju, Wyoming Game and Fish Department, personal communication).

Habitat Changes

As early as 1911, Preble (1911) noted the negative effects that elk were having on their habitat in Jackson Hole. He observed intense competition for food during winter, noting the elk "were driven to browse on the willows and other shrubs already nearly destroyed during previous winters. They soon eat the smaller twigs and then are forced by hunger to attack the bark and larger branches...."

Table 3. Cost/winter of feeding elk in several western states. Costs include feed, labor to distribute feed, and fuel costs. Costs for Idaho, Oregon, Utah, and Washington are averages for 1995–99. Costs in Utah and Wyoming were averaged for 1994–98.

State	Location (herd)	No. of elk	Cost/elk	Total cost
Idaho	Donnley	100	75	7,500
Idaho	Stanley	240	43	10,389 ^a
Idaho	Sun Valley–S. Fork Boise River	1,193	112	134,000 ^b
Idaho	Swan Valley	740	92	67,733 ^a
Idaho	Total (mean)	2,273	(81)	219,622
Oregon	Elkhorn	1,400	93	130,000
Oregon	Wenaha	523	22	11,500 ^c
Oregon	White River	350	11	4,000 ^d
Oregon	Jewel Meadows	275	47	13,000
Oregon	Total (mean)	2,548	(43)	158,500
Utah	Hardware Ranch	490	92	45,000
Washington	Yakima	3,000	39	117,500
Wyoming	National Elk Refuge (Jackson)	9,200	35	325,128
Wyoming	Alkalai (Jackson)	663	41	27,316
Wyoming	Fish Creek (Jackson)	827	48	39,696
Wyoming	Patrol Cabin (Jackson)	442	49	21,658
Wyoming	Camp Creek (Fall Creek)	628	46	28,888
Wyoming	Dog Creek (Fall Creek)	712	47	33,464
Wyoming	Horse Creek (Fall Creek)	1,137	39	44,343
Wyoming	South Park (Fall Creek)	1,150	44	50,600
Wyoming	Dell (Hoback)	232	82	19,024
Wyoming	McNeel (Hoback)	512	61	31,232
Wyoming	Grey's River (Afton)	956	58	55,448
Wyoming	Forest Park (Afton)	810	62	50,220
Wyoming	Jewett (Piney)	612	66	40,392
Wyoming	Finnegan (Piney)	386	67	25,862
Wyoming	Franz (Piney)	426	72	30,672
Wyoming	North Piney (Piney)	305	59	17,995
Wyoming	Bench Corral (Piney)	566	36	20,376
Wyoming	Black Butte (Green River)	555	76	42,180
Wyoming	Green River Lakes (Green River)	468	49	22,932
Wyoming	Soda Lake (Green River)	785	36	28,260
Wyoming	Fall Creek (Pinedale)	776	60	46,560
Wyoming	Scab Creek (Pinedale)	566	86	48,676
Wyoming	Muddy (Pinedale)	677	64	43,328
Wyoming	Total (mean)	23,391	(56)	1,094,250

^a Winter 1998–99 only.

^b Winter 1996–97 only.

^c Elk are fed only 5 times/week, and hay is harvested on site by sharecropper.

^d Elk are fed only once/week, and hay is harvested on site by sharecropper.

Haystacks about ranches are, of course, eagerly sought. When they find the stacks securely fenced, large numbers die immediately around them.”

Craighead (1952) and Murie (1944, 1951) likewise detailed the decline of palatable deciduous woody vegetation. In 1944, Murie cautioned:

There has been too much reliance on feeding of hay as a solution, rather than herd reduction to range carrying capacity. Hay

feeding concentrates the animals and is the surest way to destroy the browse of a range where it is practiced... Willows on the refuge are almost gone. Serviceberry is barely able to keep alive. Aspen groves are on the way out, and have been so heavily browsed that except for falling leaves, they no longer furnish much feed. Even many conifers here have been trimmed up so far as elk can reach.

Heavy hedging of palatable woody plants occurs adjacent to feedgrounds in Idaho, Oregon, Utah, Washington, and Wyoming. On a landscape scale, as one moves away from areas where elk are concentrated during winter, the vigor and health of woody plants improve (Kay 1985, Romme et al. 1995). Supplementally fed white-tailed deer also exhibited reduced browse utilization with distance from feeding sites (Doenier et al. 1997). Because of their size and food requirements, elk can be particularly damaging when they are concentrated near feedgrounds (Thorne and Butler 1976). They can prevent successful regeneration of aspen by annually browsing suckers and stripping bark from tree trunks (Krebill 1972, Hart and Hart 1989). Declines in aspen regeneration and growth, as elk populations have increased during the 20th century, have been reported in most Rocky Mountain national parks of the U.S. and Canada (White et al. 1998).

Following the clearcutting of aspen stands on the NER to stimulate vegetative reproduction, aspen regeneration was measured inside and outside small exclosures (Dieni et al. 2000). Post-treatment density of aspen suckers was greater within exclosures during 9 years of study. After 9 years, <5% of stems outside exclosures were >2m tall, compared to 68% of stems within exclosures. Dieni et al. (2000) concluded that repeated annual browsing by elk was suppressing aspen recruitment and growth.

Elk are primarily grazers and do quite well on a diet of herbaceous vegetation. Excessive grazing near feedgrounds was not mentioned by wildlife managers I interviewed, probably because of the limitations of deep snow on availability of herbaceous vegetation. In addition, the migratory nature of elk provide grazed plants a period of recovery during the growing season, and seasonal grazing may stimulate above-ground production (Augustine and McNaughton 1998, Frank 1998).

Heavy browsing by high concentrations of ungulates that limits growth and health of woody vegetation, however, may produce community-level consequences. Deterioration of woody plant communities may occur slowly and be imperceptible to the casual observer. Only careful monitoring may reveal cascading consequences of habitat deterioration to other biota. Western aspen communities, for example, support a highly diverse fauna, including 56 species of mammals and 135 species of birds (Flack 1976, DeByle 1985, Stelfox 1995). For most species of birds, abundance was correlated with canopy heterogeneity and successional stage of stands in Alberta.

Richness and abundance of bird species was greatest in 120+ year-old aspen stands. Mammal species richness in Alberta was also greater in old (120+ years) stands of aspen, compared to young or mature stands (Stelfox 1995). Carothers et al. (1974) reported that where ungulates reduce the vertical complexity of woody vegetation, bird species diversity is likely to decline. Berger et al. (2001) found inverse relationships between moose densities and avian diversity and abundance in willow riparian communities of the Greater Yellowstone Ecosystem. There is growing evidence that birds which use woody habitats as breeding, feeding, roosting and brood-rearing habitat are generally less abundant in habitats used by high densities of ungulates (Casey and Hein 1983, deCalesta 1994).

Changes in Elk Behavior

Among the motives for feeding elk is the desire to modify their distribution. A common motivation expressed by wildlife managers for justifying winter feeding was to prevent elk from migrating to lower elevation, more snow-free winter ranges (Table 1). Interception of fall migrations prevented elk from occupying historic winter ranges that were in private ownership. In most cases, short-stopping migrations averted elk reaching and causing damage on agricultural lands, where hay, grains, or orchards were produced, or where cattle were pastured and fed in winter. In some cases, such as the NER and Sun Valley, Idaho, the damage that elk were likely to cause would also have included ornamental plantings in residential areas.

Some feedgrounds were established on winter ranges, such as those for the Jackson elk herd in Wyoming and Wenaha in Oregon. Many others were established on transitional range between summer and winter ranges (Elkhorn and White River in Oregon, Swan Valley in Idaho, and most of the feedgrounds of the Piney, Green River, and Pinedale herds in Wyoming). Still others were located on elk summer range (Hardware Ranch, Utah, and Forest Park feedground in Wyoming).

Elk readily habituate to feeding operations. Yet if feeding is inconsistent, animals will move elsewhere to satisfy their appetites, as occurred at Yakima, Washington, when feed could not be distributed to elk during a winter storm. Thus, baiting of elk is initiated at some Wyoming feedgrounds as early as November, to keep elk from moving onto private lands, well before feeding winter maintenance rations is necessary.

Where elk are prevented from migrating to areas of more accessible forage, the hay they are fed may constitute the bulk of their diets because standing forage is buried beneath snow. Only woody plants may remain readily available to elk and subsequently suffer severe hedging. Where feedgrounds are contiguous with winter range, such as the Jackson elk herd, Yakima, Washington, and Wenaha and White River in Oregon, feeding serves to supplement elk diets with high-quality forage to control distributions and reduce winter mortality (Robbins et al. 1982).

Wildlife managers in Idaho, Oregon, and Wyoming have noted some movement of elk, from 1 winter to the next, among adjacent feedgrounds and feeding sites. Nevertheless, elk fed during winter generally display high fidelity to winter feedgrounds (Tanner 1965, Smith and Robbins 1994). Feeding likely reinforces fidelity to wintering areas (Smith 1994).

Feedground attendance and arrival at feedgrounds varies considerably with winter severity (Boyce 1989, Smith and Robbins 1994). Consequently, initiation of feeding varies with weather, particularly snow accumulations. At the NER, initiation of feeding was correlated ($R^2 = 0.96$) with December snow depths and the number of elk on the NER (Smith et al. 1997). Weather conditions also influence the composition of elk attending feedgrounds in the Jackson elk herd. When feeding began later in winter, a higher proportion of calves remained off feedgrounds. Radiocollared calves were more likely to winter off feedgrounds than were older radioed elk (Smith 1994). Calves wintering off feedgrounds had poorer winter survival than those on feedgrounds (Smith and Anderson 1998); but the negative effect on overall cohort survival was mitigated by fewer calves wintering off feedgrounds during severe winters (Smith 1994).

Other concerns about the effects of feeding on elk behavior are more subjective or emotional in nature. Clearly, feeding elk during winter is popular with much of the public. A 1994 survey of Idaho citizens revealed that 93% of hunters and 79% of nonhunters supported the Idaho Department of Fish and Game's spending money to feed big game animals during winter (Duda and Young 1994).

People viscerally relate to feeding wildlife. It is a step early humans took many times in the process of domesticating cats, dogs, horses, cattle, goats, etc. However, habituation of elk to human presence and to following feedwagons, rather than rustling for wheatgrasses, troubles some observers. As 1 wild-

life manager in Oregon observed, "Once you control the food of the critter, you control the critter."

Disease

Diseases affect the species composition of many ecosystems, and are likely to play an important role in management of wildland ecosystems in the future (Real 1996). Infectious and parasitic diseases can be important regulating mechanisms of animal populations at high densities (Anderson and May 1979, May 1983). Previous workers have suggested that overstocked ranges could lead to increased disease in ungulate populations (Cowan 1950, Murie 1951), or they have described wildlife epizootics associated with high-density populations (Matschke et al. 1984). Increased animal density results in greater demand on the finite resources of the available habitat and closer proximity of the potential hosts of disease. Consequences include poorer host nutrition and increased socio-behavioral stressors, perhaps leading to reduced immunocompetence (Sinclair 1977, Kistner et al. 1982), and increased opportunity for disease transmission through animal-to-animal contact and availability of pathogens in the environment.

Viral, bacterial, and parasitic diseases of importance among free-ranging populations of feedground elk include coronavirus and rotavirus in neonates (Smith and Anderson 1996), septicemic pasteurellosis and brucellosis (Thorne 1982*a, b*; Franson and Smith 1988; Smith and Roffe 1994), and psoroptic mange (Murie 1951, Samuel et al. 1991). Additionally, bovine viral diarrhea and bovine respiratory syncytial virus were identified in NER elk during winters 1997, 1998, and 2000 from serum antibody titers (T. Roffe, U.S. Geological Survey, unpublished data).

Psoroptic mange, or scabies, predisposes 20–30 adult male elk to die each winter on the NER (Samuel et al. 1991). Scabies in elk is of little concern to humans or the livestock industry due to the host specificity of *Psoroptes cervinus*. However, clinical scabies does affect the aesthetics of afflicted animals, and reduces the survival of trophy size bull elk and the quality of capes of harvested animals. Elk may possibly serve as a reservoir for infection of sympatric bighorn sheep populations (Lange 1982). Experimental injections of scabby bull elk with Ivermectin have produced short-term reductions of mite infestations (Muschenheim 1988). Too little is known about the host-parasite ecological relationships to provide practical management alternatives for eradication of scabies in elk.

Septicemic pasteurellosis is an acute disease of wild and domestic ruminants caused by *Pasteurella multocida*. The hemorrhagic septicemic form of pasteurellosis is an acutely fatal disease and rare on this continent. It has been reported from dairy cattle (Carter 1982) and several species of free-ranging wildlife. Pasteurellosis has occurred at Wyoming's Camp Creek feedground (S. Smith, Wyoming Game and Fish Department, personal communication). Periodic outbreaks of the disease have been documented on the NER (Thorne 1982b, Franson and Smith 1988) with the largest number of animals dying during winter 1992–93 (T. Roffe and B. Smith, unpublished data). From DNA fingerprinting, Wilson et al. (1995) suggested that *P. multocida* recovered from NER was a pathogen, rather than an opportunist bacteria. Although pasteurellosis is rarely reported elsewhere in elk (Franson and Smith 1988), feedground elk are more intensively monitored than most elk herds.

The lack of reports lends little to a conclusion regarding importance of host density in the epidemiology of septicemic pasteurellosis. The known epidemiology suggests that a wide range of factors is important. Rapid progression and usually fatal outcome of pasteurellosis makes its epidemiology quite different from brucellosis and scabies (Smith and Roffe 1994).

Bovine brucellosis is an infectious disease of cattle occurring in at least 120 countries around the world. The hallmark clinical sign of the disease is abortion. Elk may also experience synovitis and arthritis, which causes lameness in some infected animals (Thorne 1982a). Transmission is by direct contact with *Brucella abortus* contaminated reproductive products associated with abortion or birth.

A national brucellosis eradication program has nearly eliminated brucellosis in cattle in the United States. Since the 1980s, eradication efforts have focused on the potential for wild bison and elk to transmit brucellosis to cattle herds (Cheville et al. 1998). Elk may have contracted brucellosis from infected cattle shipped from Europe (Tunicliff and Marsh 1935), or secondarily from American bison (*Bison bison*) that were initially infected by the cattle (Thorne 1982a). In North America, significant levels of brucellosis in wild elk occur only in Greater Yellowstone Ecosystem (Thorne and Herriges 1992). Bison in Yellowstone National Park and bison that were introduced to Jackson Hole and winter on the NER are also infected with brucellosis (Williams et al. 1993).

Seroprevalence among adult female elk in the western Wyoming feedground complex has

averaged 37% since 1970 (Thorne and Herriges 1992). During herd reductions of the 1960s, 1.7% of 6,027 elk on Yellowstone National Park's northern range were brucellosis test reactors (Smith and Robbins 1994). Elsewhere, 2 of 178 Wyoming elk not associated with feedgrounds tested positive in 1990 (Thorne and Herriges 1992). Brucellosis is absent or at nonsignificant levels of prevalence in other states (Smith and Roffe 1994), with the exception of eastern Idaho, where elk on 2 feedgrounds tested positive in 1998 and 1999.

Experiments conducted at the NER indicated that abortion could potentially reduce the annual calf crop by 7% (Oldemeyer et al. 1993). However, the primary concern is the potential for transmission of brucellosis to domestic cattle raised within the distribution of elk herds in the Yellowstone Ecosystem. USDA regulations that restrict sale and shipment of brucellosis-infected cattle and domesticated bison create concerns about financial hardship among agricultural interests in Wyoming, Montana, and Idaho that harbor infected wild bison and elk. Litigation against state and federal wildlife management agencies, and threatened livestock market sanctions against those states, are among the recent repercussions of wildlife brucellosis.

Although elk and bison have experimentally transmitted brucellosis to cattle in confined conditions, transmission of brucellosis from elk to cattle under field conditions has not been documented (Thorne and Herriges 1992). High animal densities that occur on feedgrounds are necessary for transmission and maintenance of a high prevalence of brucellosis in elk (Thorne et al. 1996).

Olaus Murie, who first discovered brucellosis in Wyoming elk in 1930, could not have envisioned the consequences that feeding elk would produce. The costs, controversies, lawsuits, and ill feelings that brucellosis has caused are well documented (Keiter and Froelicher 1993, Carlman 1994, Brimmer 1999). For a disease that is relatively benign in elk, brucellosis has whipped up a firestorm that has spread to the highest levels of state and federal government. The predictable spin-offs of interagency committees, environmental assessments, environmental impact statements, feedground management plans, and innumerable research efforts create work and consume dollars that are often redirected from wildlife and habitat management programs. Most recently, the state of Wyoming sued the federal government to assert authority over wildlife on the NER in order to force vaccination of elk.

The 1999 federal court ruling on the case found for the federal government, reasserting the statutory authority of the Secretary of the Interior over wildlife on national wildlife refuge lands (Brimmer 1999). That ruling is under appeal.

Brucellosis has elevated the feeding issue to a new level of public awareness. More citizens question the justification for feeding when the practice is responsible for the spread and maintenance of disease in elk.

Biologically, brucellosis is a red flag. It warns us that out of a million elk in North America, only those associated with the winter feeding programs in western Wyoming and adjacent eastern Idaho maintain this disease at any significant prevalence. It warns us that the conditions experienced by elk concentrated on feedgrounds are ripe for the transmission of other, more pathogenic diseases. Brucellosis is difficult to maintain in a free-ranging population of elk, due to the restricted route of transmission of the bacterium in reproductive products. Other diseases that could be spread through mutual grooming, shared food, and aerosol would spread more rapidly through an immunologically naïve host population. These include diseases such as bovine tuberculosis, which devastated elk game farms in western Canada and the United States in the early 1990s (Roffe and Smith 1992), and chronic wasting disease. The latter is poorly understood, has varietal forms that affect a variety of mammals (including cattle and humans), is popping up in game farms in the western United States and Canada, and is in wild populations of elk and mule deer of southeastern Wyoming and northern Colorado (Williams and Young 1993). Should either disease become established within the Greater Yellowstone Ecosystem, the number of infected herds could rapidly expand. Twenty-five herds totaling 120,000 elk and 2 herds totaling 3,000 bison winter in the 7 million ha Greater Yellowstone Ecosystem (Toman et al. 1997). Because distributions of adjacent herds overlap, generally during summer and fall, bovine tuberculosis or chronic wasting disease could spread to many herds (Fig. 3).

In cooperation with federal land management agencies and the Rocky Mountain Elk Foundation, the Wyoming Game and Fish Department has been addressing the brucellosis–feedground issue by conducting elk winter habitat improvement projects. The Wyoming Game and Fish Department also implemented a brucellosis vaccination program in 1985 at the Grey's River feedground. Although it is debatable whether the Strain 19 vaccine developed

for cattle is effective in elk (Peterson 1991), the program has expanded to 21 of the state's 22 elk feedgrounds (Thorne and Herriges 1992).

Keiter and Froelicher (1993) reviewed the lawsuit brought against the federal government by Parker Land and Cattle Company and the suit's fallout. They suggested that the only fully effective means of eradicating brucellosis from the Greater Yellowstone Ecosystem's elk and bison populations would be depopulation, "an extreme policy choice, with serious political, ecological, and economic repercussions." They went on to say that, "In Wyoming, at least, any effective response to wildlife brucellosis will almost certainly require reduction—if not elimination—of the elk feedgrounds, which will undoubtedly impact elk population numbers and hunting opportunities." Given the polarization and politicization of the brucellosis issue, they advocated a regional brucellosis control policy based on the principle of risk reduction, not disease eradication.

In 1994, the Greater Yellowstone Interagency Brucellosis Committee (GYIBC) was formed. It is comprised of land management, wildlife management, and agricultural agencies from the federal

YELLOWSTONE ECOSYSTEM

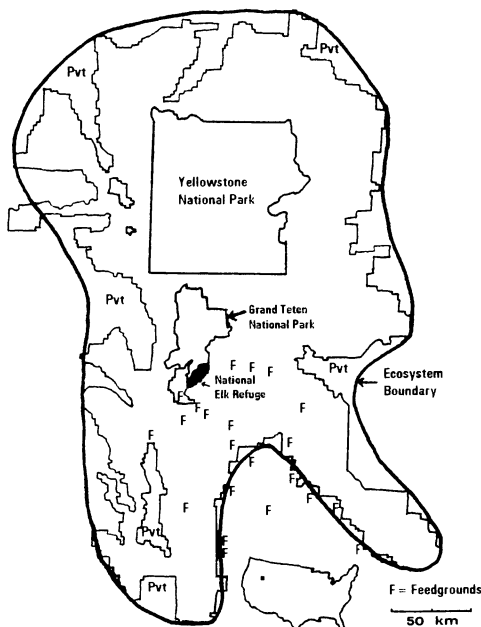


Fig. 3. Distribution of winter feeding of elk at 22 Wyoming feedgrounds and the National Elk Refuge in the Greater Yellowstone Ecosystem. Shown also is the distribution of private lands (Pvt) within the 7 million-ha ecosystem, which largely consists of public lands.

government and the states of Idaho, Montana, and Wyoming. The GYIBC meets 3 times each year to coordinate brucellosis research and public information efforts. A position statement developed and adopted by the GYIBC in 1994 recognizes the link between concentration of ungulates at feedgrounds and disease problems. The statement concludes, "...the GYIBC strongly recommends that winter feeding of elk should be discouraged, and no additional public or private feedgrounds be established in the Greater Yellowstone Area. Establishment of emergency or permanent feedgrounds for other wild ungulates, which may act as an attractive nuisance and concentrate elk or bison, is likewise discouraged."

ALTERNATIVES TO FEEDING

Winter feeding of elk can be viewed as a means of conflict resolution, generally spawned by intense public pressure. It is not based on scientific principle and sustainable resource management policy. Administrators may see winter feeding as the least painful remedy for producing immediate results to appease differing groups: agricultural interests that desire rapid resolution to crop damage, and pro-wildlife constituencies that oppose reductions in elk populations despite wildlife-human conflicts or dwindling habitat. As such, winter feeding fits comfortably into the context in which wildlife management developed as an agricultural paradigm that employed simplified concepts of ecosystems in an effort to produce abundant numbers of certain species for harvest (Lancia et al. 1996).

The potential for spread and maintenance of epizootic disease in artificially crowded elk populations, as evidenced by brucellosis in Greater Yellowstone Ecosystem feedgrounds and bovine tuberculosis and chronic wasting disease in North American game farms, argues for a shift from a production-consumption model of elk management toward an ecological paradigm advocated for the wildlife profession (Lancia et al. 1996). Leopold's (1966) philosophy of conservation matured from the production of preferred species to an appreciation of the land as a complex organism of interdependent and necessary components. This shift moved the wildlife profession beyond single-species management to embrace conservation for all species, maintenance of ecosystem functions, and sustainability of resources (Holt and Talbot 1978).

Except for limited supplemental feeding of elk in northern Utah during the 1940s and 1950s, the

only location in which termination of feeding programs conducted by a state or provincial agency has been attempted is Idaho's Swan Valley. Although the Idaho Fish and Game Department advocated phasing out that elk feeding program previously, public pressures perpetuated the feeding until 1998. With the discovery of brucellosis in elk tested at Rainy and Conant Creek feedgrounds, the governor of Idaho appointed a task force to make recommendations on management of elk. This task force, composed of state officials and private citizens, recommended reduction of elk numbers and elimination of the feeding programs. The threat of brucellosis transmission from elk to area cattle herds was the driving force (Dave Koehler, Idaho Fish and Game Department, personal communication). A herd management plan has been developed, with public input, to liberalize elk seasons and bring elk numbers in balance with available winter range and to reduce crop depredations. Improvements of elk winter habitat on public lands are intended to perpetuate huntable elk herds in Swan Valley. Winter feeding continues for the next several years in Swan Valley, while elk are trapped at feedgrounds and translocated to alternative winter ranges.

It may not seem so in the face of a tide of public and political pressures that rise in support of initiating feeding, but it is easier to not begin feeding elk than it is to terminate a feedground once it is established. Some feeding programs arose from an emergency or temporary situation, rather than with the intent of feeding elk on a long-term basis. A severe winter, a summer drought, or an unusual movement of elk to private farm or ranchlands may have prompted a state agency to reduce anticipated winter mortality or bait elk away from private lands. In other cases, private feeding of elk became public feeding of elk when pleas from landowner or legislator prompted the state agency to assume the responsibility to feed hay-conditioned animals. "Emergency" situations are susceptible to varying interpretations. Once elk are fed during a tough winter, public expectation may render most winters emergencies. Guidelines to define what constitutes an emergency, such as those developed in Colorado that specify when feeding is necessary to prevent high losses of female elk or deer, must exist before emergencies are declared.

Alternatives to winter feeding of elk are largely recognition that wildlife management is people management. People, via activities and use of the landscape, affect wildlife. We influence animal

distributions and the capacity of land to sustain populations when we usurp and fragment open spaces. Subdivisions, fences, agricultural plantings, roads, and commercial developments alter the capacity of elk winter ranges to sustain populations or create conflicts that humans find unacceptable. The notion of maintaining population levels in the face of the erosion of habitat is simply unrealistic, at least from an ecological perspective. Manipulating elk populations in ways that border on semi-domestication, such as feeding and fencing them, may permit numbers to be artificially maintained on an eroded habitat base, but at what costs?

A number of actions can be taken before feeding programs are established to avoid artificial maintenance of elk herds: (1) Control elk numbers to keep them within the capacity of habitats to sustain them on a long-term basis. This is a basic tenet of sound wildlife stewardship (Leopold 1933). (2) Practice land-use planning that truly integrates the needs of elk populations. This includes avoiding encroachment of subdivisions and other development onto winter range, and adopting regulations that discourage people and dogs from harassing elk on winter ranges. (3) Avoid fragmentation of elk ranges that short-stops migration routes between summer and winter ranges. This requires conserving migration corridors as well as winter habitats. (4) Use techniques that maintain or improve the productivity of elk winter ranges. This includes forage production enhancement through prescribed burning, seeding of degraded rangelands, proper stocking of livestock if such grazing occurs on elk winter ranges, and control of noxious weeds that may compete with forage species valued by elk.

Many elk winter ranges on public lands border private lands or are a composite of private and public ownership. This clearly complicates elk conservation and increases the risk of conflict between public resource stewardship and private property rights. Fee title purchase of critical winter ranges, and land exchanges that trade public lands or their mineral rights for private lands, have served to consolidate and preserve winter ranges for the public good. Short of land acquisition, conservation easements may serve to maintain private lands in private ownership and accomplish public resource objectives. In other cases, cooperative ventures between public agencies and private landowners can promote the value of private lands as elk winter range by compensating landowners for accommodating wildlife. These ventures may include compensating landowners for production

and reservation of standing elk feed, or by landowners charging hunters access fees.

PERCEPTION AND STEWARDSHIP

In a recent essay, Dave Stalling (1998) wrote, "As throngs of people settle where elk once wintered, fostering a piecemeal whittling of habitat, wildlife management options dwindle. Alternatives to winter feeding decline, social pressures mount, biopolitics expands, and elk grow less wild."

Indeed, the surest path to keeping the wild in wildlife is to maintain wildlands. This, unfortunately, is easier said than done because Americans are in the midst of a pilgrimage from the metropolis to the mountains. One justification that has been put forward for feeding elk during winter is that summer ranges are stocked below carrying capacity. Lovass (1970) points out that feeding elk is an effort to have more elk than the range will support. He adds that feeding can at best only compound the existing imbalance between elk and range. Boyce (1989) contends that winter feeding of the Jackson elk herd is justified. He reasons that, "only winter range is out of balance, and this is due to human encroachment." True enough. But following this dictum, there remain fewer and fewer places in western North America where winter feeding of elk is then not justified.

Elk habitat is wildlife habitat. As noted above, too many elk can degrade habitats used by many species of wildlife. Likewise, loss of elk winter range to occupation and use by humans displaces not only elk, but wildlife in general. Although the elk may be fed on an adjacent site, other species may experience a net loss in the land's capacity to sustain them. The more that wildlife officials feed the animals, the more the public may accept feeding as mitigation for development. This erosion of habitat, the currency of wildlife, confronts and frustrates town and county planners throughout the West. Good intentions to maintain open space and the integrity of winter ranges are overwhelmed by the rising value of real estate advertised "with wildlife right in your backyard." Sustainability of elk, warblers, and willows depends on public and private stewardship of wildlife real estate. Leopold (1966) articulated this stewardship responsibility several decades ago: "We abuse land because we regard it as a commodity to us. When we see land as a community to which we belong, we may begin to use it with love and respect."

Creative opportunities for habitat conservation still abound. They meld the goodwill of landowners and private citizens and the use of public and

private funds. Prime examples are recent efforts to secure winter range for Yellowstone's northern elk herd in Montana (McMillion 1999). However, as time passes, opportunities to protect elk winter ranges for the long-term sustainability of herds likewise pass. Ultimately, 2 questions should be answered when considering whether winter feeding, or an alternative solution, should be pursued to maintain elk in a conflict situation. What are the inherent economic, ecological, and political costs? Is this solution sustainable?

THE ROLE OF SCIENCE

Sinclair (1991) contended that wildlife management and research are not separate entities. He cautioned that management lacking the application of the scientific method leads to mismanagement through acceptance of untested hypotheses as dogma. Through the inductive scientific method of seeking knowledge (Romesburg 1981), managers may conclude and advocate that the long-term feeding programs in western Wyoming have maintained large numbers of elk on diminished habitat and that those programs have reduced expected wildlife-human conflicts, in contrast to not feeding. It is not surprising then that elk feeding programs are generally well supported by sportsmen and agricultural interests for these immediate benefits. Similarly, managers may inductively reason that the liabilities apparently associated with crowding elk on feedgrounds, including budgetary costs, habitat changes, behavioral changes in elk, and disease, would not occur in the absence of feeding. These positive and negative associations are correlative. Although based on years of observations, they provide administrators, managers, and the public scant and potentially unreliable information about the comparative utility of alternative management approaches. Without rigorously testing alternative methods for managing human-wildlife conflicts, we cannot reliably conclude that winter feeding is the best, or worst, solution for elk or the ecosystems they inhabit.

Conducting management experiments to test and learn from alternative approaches to management problems in which there is a high degree of uncertainty about outcomes, or a high degree of risk associated with incorrect decisions, allows administrators and managers to evaluate alternatives and to improve decision-making. Conducted as rigorous experiments using the hypothetico-deductive process (Romesburg 1981, Murphy and Noon 1991), researchers can increase knowledge

of wildlife systems and managers can evaluate management alternatives and provide the public better rationales for decisions on complex issues.

Given the weight of socioeconomics and politics, could this adaptive management approach to decision-making be applied to elk-human conflict resolution? Perhaps. Where conflicts arise in 2 or more similar situations, alternative management approaches could be tested experimentally. One alternative may endorse winter feeding, another may use public-private partnerships to plan and promote habitat improvements and conservation to maintain populations. Careful formulation and testing of hypotheses of individual, population, and community-level effects, as well as socioeconomic consequences, would benefit future decision-making with respect to whether elk should or should not be fed during winter. However, given the liabilities of feeding and the difficulty of terminating ongoing feeding programs, I could justify initiating a new feeding program only if such a policy decision was inevitable and experimentation was a consensus function of its use.

Another possible application of adaptive resource management to winter feeding of elk exists in the western Wyoming feedground complex. These ongoing programs afford an opportunity to compare management alternatives to remedy the brucellosis disease issue (Peterson 1991). Elk in all feedgrounds are infected with brucellosis, and vaccination against brucellosis occurs at 21 of 22 state feedgrounds. Hypotheses about prevalence of brucellosis and other population process variables could be formulated and tested to compare elk using feedgrounds and elk for which 1 or more feedgrounds are phased out. For the former, feeding and vaccination of elk would continue. For the latter experimental groups, management may include any of the 4 strategies listed previously, as well as reestablishing elk migrations to historic winter ranges on public lands (Allred 1950). Such experiments with free-ranging populations of animals are complicated and run inherent risks of failure resulting from lack of administrative commitment to the experiment. Nonetheless, applied as adaptive management, managers are not committed to a single model and can consider the merits of 2 or more models simultaneously. Importantly, adaptive management can also lead to evaluation of values and implicit assumptions that often underlie existing management policies (Lancia et al. 1996).

Proactive testing of management alternatives may avert crisis management. Ultimately, agencies

that have elected winter feeding to resolve elk-human conflicts may be forced to examine that choice subsequent to changes in public values, legal challenges, or disease in feedground elk. The loss of Michigan's tuberculosis-free status for cattle, following the state's tuberculosis epizootic in white-tailed deer, compelled the state government to ban private feeding of deer and launch substantial reductions in the infected deer population. Such events can preempt careful evaluation of management alternatives, potentially at the expense of agency credibility and precious public resources.

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LITERATURE CITED

- ALBON, S. D., T. H. CLUTTON-BROCK, AND F. E. GUINNESS. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology* 56:69-81.
- ALLRED, W. J. 1950. Re-establishment of seasonal elk migration. *Transactions of the North American Wildlife Conference* 15:597-611.
- ANDERSON, C. C. 1958. The elk of Jackson Hole. *Wyoming Game and Fish Commission Bulletin* 10.
- ANDERSON, R. M., AND R. M. MAY. 1979. Population biology of infectious diseases: part I. *Nature* 280:371-377.
- AUGUSTINE, D. J., AND S. J. MCNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-1183.
- BAILEY, J. R. 1999. A working model to assist in determining initiation of supplemental feeding of elk and a carrying capacity model for the National Elk Refuge, Jackson, Wyoming. Thesis, University of Wyoming, Laramie, USA.
- BERGER, J., P. B. STACEY, L. BELLIS, AND M. P. JOHNSON. 2001. A mammalian predator-prey disequilibrium: how the extinction of grizzly bears and wolves affects the biodiversity of avian neotropical migrants. *Ecological Applications*: in press.
- BETTS, R. B. 1978. Along the ramparts of the Tetons: the saga of Jackson Hole, Wyoming. University of Colorado, Boulder, USA.
- BOYCE, M. S. 1989. The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, Cambridge, United Kingdom.
- BRIMMER, C. A. 1999. State of Wyoming versus USA. Number 98-CV-037B, District Court of Wyoming, Cheyenne, USA.
- BUBENIK, A. B. 1982. Physiology. Pages 125-179 in J. W. Thomas and D. E. Toweill, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- BUNNELL, S. D. 1995. Status of elk in North America. Rocky Mountain Elk Foundation Special Report 1, Missoula, Montana, USA.
- CARLMAN, L. R. 1994. Wildlife-private property damage law. *Land and Water Law Review* 29:89-115.
- CAROTHERS, S. W., R. R. JOHNSON, AND S. W. AITCHISON. 1974. Population structure and social organization of southwestern riparian birds. *American Zoology* 14:97-108.
- CARTER, G. R. 1982. Whatever happened to hemorrhagic septicemia? *Journal of the American Veterinary Association* 180:1176-1177.
- CASEY, D., AND D. HEIN. 1983. Effects of heavy browsing on a bird community in a deciduous forest. *Journal of Wildlife Management* 47:820-836.
- CHEVILLE, N. F., D. R. McCULLOUGH, AND L. R. PAULSON. 1998. Brucellosis in the Greater Yellowstone Area. National Research Council, National Academy Press, Washington, D.C., USA.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.
- , M. MAJOR, AND F. E. GUINNESS. 1985. Population regulation in male and female red deer. *Journal of Animal Ecology* 54:831-846.
- COWAN, I. MCT. 1950. Some vital statistics of big game on overstocked mountain range. *Transactions of the North American Wildlife Conference* 15:581-588.
- CRAIGHEAD, J. J. 1952. A biological and economic appraisal of the Jackson Hole elk herd. New York Zoological Society and the Conservation Foundation, New York, USA.
- DEAN, R. E., E. T. THORNE, AND I. J. YORGASON. 1976. Weights of Rocky Mountain elk. *Journal of Mammalogy* 57:186-189.
- DEBYLE, N. V. 1985. Wildlife. Pages 135-152 in N. V. DeByle and R. P. Winokur, editors. *Aspen: ecology and management in the western United States*. U.S. Forest Service General Technical Report RM-119.
- DECALESTA, D. S. 1994. Impact of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58:711-718.
- DIENI, J. S., B. L. SMITH, R. L. ROGERS, AND S. H. ANDERSON. 2000. The effects of ungulate browsing on aspen regeneration in northwest Wyoming. *Intermountain Journal of Science* 6:49-55.
- DOENIER, P. B., G. D. DELGUIDICE, AND M. R. RIGGS. 1997. Effects of winter supplemental feed on browse consumption by white-tailed deer. *Wildlife Society Bulletin* 25:235-243.
- DUDA, M. D., AND K. C. YOUNG. 1994. Idaho residents' opinions and attitudes toward the Idaho Department of Fish and Game. Unpublished report. Responsive Management, Harrisonburg, Virginia, USA.
- FLACK, J. A. D. 1976. Bird populations of aspen forests in western North America. *Ornithological Monographs* 19:1-97.
- FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. *Canadian Wildlife Service Report* 11.
- FRANK, D. A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. *Wildlife Society Bulletin* 26:410-418.

- FRANSON, J. C., AND B. L. SMITH. 1988. Septicemic pasteurellosis in elk (*Cervus elaphus*) on the United States National Elk Refuge, Wyoming. *Journal of Wildlife Diseases* 24:715-717.
- GRAVES, H. S., AND E. W. NELSON. 1919. Our national elk herds. U.S. Department of Agriculture Circular 51.
- HART, J. H., AND D. L. HART. 1989. Effect of elk on aspen ecology in Rocky Mountain ecosystems. *Bulletin of the Ecological Society of America* 70:134-135.
- HOLT, S. J., AND L. M. TALBOT. 1978. New principles for the conservation of wild living resources. *Wildlife Monographs* 59.
- HORNADAY, W. T. 1931. Thirty years war for wildlife. Charles Scribner's Sons, New York, USA.
- HOUSTON, D. B. 1982. The northern Yellowstone elk. MacMillan Press, New York, USA.
- KAY, C. E. 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. Pages 131-160 in G. W. Workman, editor. *Western elk management: a symposium*. Utah State University, Logan, USA.
- KEITER, R. B., AND P. H. FROELICHER. 1993. Bison, brucellosis, and law in the Greater Yellowstone Ecosystem. *Land and Water Law Review* 28:1-75.
- KIMBALL, J. F., AND M. L. WOLFE. 1979. Continuing studies of the demographics of a northern Utah elk population. Pages 20-28 in M. S. Boyce and L. D. Hayden-Wing, editors. *North American elk: ecology, behavior and management*. University of Wyoming, Laramie, USA.
- , AND ———. 1984. Elk management opportunities in northern Utah: to feed or not to feed. Pages 191-197 in G. W. Workman, editor. *Western elk management symposium*. Utah State University, Logan, USA.
- KISTNER, T. P., K. R. GREER, D. E. WORLEY, AND O. A. BRUNETTI. 1982. Diseases and parasites. Pages 181-217 in J. W. Thomas and D. E. Towell, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- KOZAK, H. M., R. J. HUDSON, AND L. A. RENECKER. 1994. Supplemental winter feeding. *Rangelands* 16:153-156.
- KREBILL, R. G. 1972. Mortality of aspen on the Gros Ventre elk winter range. U.S. Forest Service Research Paper INT-129.
- KREEGER, T. J., E. S. WILLIAMS, AND D. J. MONEY. 2001. *Brucella abortus* and other potential exotic diseases as a threat to indigenous species in the Greater Yellowstone Ecosystem. Fifth Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Yellowstone National Park, Wyoming, USA:in press.
- LANCIA, R. A., C. E. BRAUN, M. W. COLLOPY, R. D. DUESSER, J. G. KIE, C. J. MARTINKA, J. D. NICHOLS, T. D. NUDDS, W. R. PORATH, AND N. G. TILGHMAN. 1996. ARM! For the future: adaptive resource management in the wildlife profession. *Wildlife Society Bulletin* 24:436-442.
- LANGE, R. E. 1982. Psoroptic scabies. Pages 244-247 in E. T. Thorne, N. Kingston, W. R. Jolley, and R. C. Bergstrom, editors. *Diseases of wildlife in Wyoming*. Second edition. Wyoming Game and Fish Department, Cheyenne, USA.
- LEEK, S. N. 1909. The starving elk of Wyoming. *Outdoor Life* 77:14.
- LEOPOLD, A. 1933. *Game management*. Charles Scribner's Sons, New York, USA.
- . 1966. *A Sand County almanac with essays on conservation from Round River*. Oxford University Press, New York, USA.
- LOVASS, A. L. 1970. *People and the Gallatin elk herd*. Montana Fish and Game Department, Helena, USA.
- MATSCHKE, G. H., K. A. FAGERSTONE, F. A. HAYES, W. PARKER, D. O. TRAINER, R. F. HURL, AND V. F. NETTLES. 1984. Population influences. Pages 69-188 in L. K. Halls, editor. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- MAY, R. M. 1983. Parasitic infections as regulators of animal populations. *American Scientist* 71:37-43.
- MCCORQUODALE, S. M. 1989. Antler characteristics in a colonizing elk population. *Journal of Wildlife Management* 53:618-621.
- MCMILLION, S. 1999. Good dealing protects the Royal Teton Ranch. *Bugle* 16:12.
- MECH, L. D., M. E. NELSON, AND R. E. MCROBERTS. 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. *Journal of Mammalogy* 72:146-151.
- MITCHELL, B., D. MCCOWAN, AND I. A. NICHOLSON. 1976. Annual cycles of body weight and condition in Scottish red deer. *Journal of Zoology, London* 180:107-127.
- MURIE, O. J. 1944. Our big game in winter. *Transactions of the North American Wildlife Conference* 9:173-176.
- . 1951. *The elk of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- MURPHY, D. D., AND B. D. NOON. 1991. Coping with uncertainty in wildlife biology. *Journal of Wildlife Management* 55:773-782.
- MUSCHENHEIM, A. 1988. Ivermectin for the treatment of psoroptic scabies in elk (*Cervus elaphus nelsoni*) and Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). Thesis, University of Wyoming, Laramie, USA.
- NELSON, J. R., AND T. A. LEEGE. 1982. Nutritional requirements and food habits. Pages 323-368 in J. W. Thomas and D. E. Towell, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- OLDEMEYER, J. L., R. L. ROBBINS, AND B. L. SMITH. 1993. Effect of feeding level on elk weights and reproductive success at the National Elk Refuge. Pages 64-68 in R. Callas, D. Koch, and E. Loft, editors. *Western states and provinces elk workshop*. California Fish and Game Department, Eureka, USA.
- OZOGA, J. J. 1987. Maximum fecundity in supplementally-fed northern Michigan white-tailed deer. *Journal of Mammalogy* 68:878-979.
- PETERSON, M. J. 1991. Wildlife parasitism, science, and management policy. *Journal of Wildlife Management* 55:782-789.
- PREBLE, E. A. 1911. Report on condition of elk in Jackson Hole, Wyoming, in 1911. U.S. Department of Agriculture Biological Survey Bulletin 40:1-23.
- REAL, L. A. 1996. Sustainability and the ecology of infectious diseases. *Bioscience* 46:88-97.
- ROBBINS, R. L., D. E. REDFEARN, AND C. P. STONE. 1982. Refuges and elk management. Pages 479-507 in J. W. Thomas and D. E. Towell, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- ROFFE, T., AND B. SMITH. 1992. Tuberculosis: will it infect our elk? *Bugle* 9:86-95.
- ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. *Journal of Wildlife Management* 45:293-313.

- ROMME, W. H., M. G. TURNER, L. L. WALLACE, AND J. S. WALKER. 1995. Aspen, elk, and fire in northern Yellowstone National Park. *Ecology* 76:2097–2106.
- SADLER, R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London, England, United Kingdom.
- SAMUEL, W. M., D. A. WELCH, AND B. L. SMITH. 1991. Ectoparasites from elk (*Cervus elaphus nelsoni*) from Wyoming. *Journal of Wildlife Diseases* 27:446–451.
- SETON, E. T. 1927. Lives of game animals. Volume 3, part 1. Doubleday, Page and Company, Garden City, New York, USA.
- SINCLAIR, A. R. E. 1977. The African buffalo—A study of resource limitations of populations. University of Chicago Press, Chicago, Illinois, USA.
- . 1991. Science and the practice of wildlife management. *Journal of Wildlife Management* 55:767–773.
- SINGER, F. J., A. T. HARTING, AND K. K. SYMONDS. 1997. Density-dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12–25.
- SMITH, B. L. 1994. Population regulation of the Jackson elk herd. Dissertation, University of Wyoming, Laramie, USA.
- . 1997. Antler size and winter mortality of elk: effects of environment, birth year, and parasites. *Journal of Mammalogy* 79:1038–1044.
- , AND S. H. ANDERSON. 1996. Patterns of neonatal mortality of elk in northwestern Wyoming. *Canadian Journal of Zoology* 74:1229–1237.
- , AND ———. 1998. Juvenile survival and population regulation of the Jackson elk herd. *Journal of Wildlife Management* 62:1036–1045.
- , AND R. L. ROBBINS. 1994. Migrations and management of the Jackson elk herd. National Biological Survey Resource Publication 199.
- , ———, AND S. H. ANDERSON. 1996. Adaptive sex ratios: another example? *Journal of Mammalogy* 77:818–825.
- , ———, AND ———. 1997. Early development of supplementally fed, free-ranging elk. *Journal of Wildlife Management* 61:27–39.
- , AND T. J. ROFFE. 1994. Diseases among elk of the Yellowstone ecosystem, U.S.A. Pages 162–166 in W. van Hoven, J. Ebedes, and A. Conroy, editors. Third International Wildlife Ranching Symposium. Centre for Wildlife Management, University of Pretoria Press, Pretoria, South Africa.
- STALLING, D. 1998. A winter quandary: to feed or not to feed? *Bugle* 15:62–71.
- STELFOX, J. B., editor. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta, and Canadian Forest Service (Project 0001A), Edmonton, Canada.
- TABER, R. D. 1959. Development of the cervid antler as an index of late winter physical condition. *Proceedings of the Montana Academy of Sciences* 18:27–28.
- , K. RAEDEKE, AND D. A. MCCAUGHNAN. 1982. Population characteristics. Pages 279–300 in J. W. Thomas and D. E. Towell, editors. The elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.
- TANNER, D. 1965. The Big Wood River elk herd. *Idaho Wildlife Review* 18:3–6.
- TAYLOR, D. T., E. B. BRADLEY, AND M. M. MARTIN. 1981. The outfitting industry in Teton County: its clientele and economic importance. Agricultural Extension Service Publication B-793, University of Wyoming, Laramie, USA.
- THORNE, E. T. 1982a. Brucellosis. Pages 54–63 in E. T. Thorne, N. Kingston, W. R. Jolley, and R. C. Bergstrom, editors. Diseases of wildlife in Wyoming. Second edition. Wyoming Game and Fish Department, Cheyenne, USA.
- . 1982b. Pasteurellosis. Pages 72–77 in E. T. Thorne, N. Kingston, W. R. Jolley, and R. C. Bergstrom, editors. Diseases of wildlife in Wyoming. Second edition. Wyoming Game and Fish Department, Cheyenne, USA.
- , D. ABENDROTH, S. KILPATRICK, AND S. SMITH. 1996. Beating brucellosis. *Wyoming Wildlife* 60:17–24.
- , AND G. BUTLER. 1976. Comparison of pelleted, cubed, and baled alfalfa hay as winter feed for elk. Wyoming Game and Fish Department Technical Report 6.
- , AND J. D. HERRIGES. 1992. Brucellosis, wildlife and conflicts in the Yellowstone area. Transactions of the North American Wildlife and Natural Resources Conference 57:453–465.
- TOMAN, T. L., T. LEMKE, L. KUCK, B. L. SMITH, S. G. SMITH, AND K. AUNE. 1997. Elk in the Greater Yellowstone Area: status and management. Pages 56–64 in E. T. Thorne, M. S. Boyce, P. Nicoletti, and T. J. Kreeger, editors. Brucellosis, bison, elk, and cattle in the Greater Yellowstone Area: defining the problem, exploring solutions. Pioneer Printing, Cheyenne, Wyoming, USA.
- TREFETHEN, J. B. 1961. Crusade for wildlife: highlights in conservation progress. Stackpole Books, Harrisburg, Pennsylvania, USA.
- TUNICLIFF, E. A., AND H. MARSH. 1935. Bang's disease in bison and elk in the Yellowstone National Park and the National Bison Range. *Journal of American Veterinary Medical Association* 146:225.
- WHITE, C. A., C. E. OLMSTED, AND C. E. KAY. 1998. Aspen, elk and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* 26:449–462.
- WILBRECHT, J. E., AND R. L. ROBBINS. 1979. History of the National Elk Refuge. Pages 248–255 in M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, USA.
- WILLIAMS, E. S., E. T. THORNE, S. L. ANDERSON, AND J. D. HERRIGES. 1993. Brucellosis in free-ranging bison (*Bison bison*) from Teton County, Wyoming. *Journal of Wildlife Diseases* 29:118–122.
- , AND S. YOUNG. 1993. Neuropathology of chronic wasting disease of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). *Veterinary Pathology* 30:36–45.
- WILSON, M. A., R. M. DUNCAN, T. J. ROFFE, G. E. NORDHOLM, AND B. M. BERLOWSKI. 1995. Pasteurellosis in elk (*Cervus elaphus*): DNA fingerprinting of isolates. *Veterinary Research* 137:195–196.
- WOLFE, G. J. 1983. The relationship between age and antler development in wapiti. Pages 29–36 in R. D. Brown, editor. Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.