INTRODUCTION

I will discuss predator-prey relationships in a management context; I emphasize management because it is management of predator-prey systems that produces controversy and led to this symposium.

My focus is on systems with wolves, black bears, and grizzly bears as predators and moose and caribou as primary prey. Deer-wolf systems in southeast Alaska are briefly mentioned. I have chosen systems where predators are or were largely lightly exploited; that is, predators were able to more or less seek their own level of abundance. However, there were brief periods of predator control from which we learned about predator-prey relationships.

This paper addresses 3 topics:

1. Why manage predator-prey systems?
2. How predation reduces prey abundance.

I will not dwell on details of individual studies; instead I will use data from several studies to make specific points. Let's begin.

WHY MANAGE PREDATOR-PREY SYSTEMS?

Why manage predator-prey systems? I think the answer is simple—man wants something that unmanaged systems do not provide.

What does man ask from wildlife? How does he use wildlife? For the most part, use falls in 4 four major categories:
1. Viewing and photography—These are major uses of wildlife in Alaska. You only have to look at the flow of people through Denali National Park to realize this. People also extensively use areas outside our parks.

2. Hunting—Hunting for recreation and for trophies is also a major use of wildlife by Alaskans.

3. Food—Wildlife provides sustenance for rural people and many urban people.

4. Spiritual—Spiritual use of wildlife goes far back into human culture and is easily recognized in the totem poles and masks of native Americans. However, wildlife has spiritual qualities for a growing number of urban Americans.

Why are these uses or demands for wildlife sometimes hard to provide? Why must these uses be periodically managed for rather than being by-products of unmanaged systems? The answer is: natural processes sometimes limit prey and predators at low densities. Wildlife at low densities can sustain little use by man—either for viewing or for hunting. Predators play a large role in determining prey abundance, and thus, their own abundance. The consequence of little or no management of predators in predator-prey systems with 2 or 3 predator species is sometimes prolonged low use of wildlife.

Other speakers at the symposium provided examples of predation maintaining prey at low densities in Canada. Let us look at some examples of long periods of low animal abundance in Alaska; predation had a large effect in some of these examples.

Before I present the examples, I want you to realize that I am going to discuss principally predator-prey relationships here. Do not think I dismiss hunting, weather, and nutrition as powerful forces—they are. They play important roles in the dynamics of predator-prey systems. But, because of the short time, I will concentrate on predation.

Let us look at 3 examples where prey populations have declined and remained at low densities for extended periods.

1. Moose abundance in interior Alaska is characterized by long periods of relatively low density during this century (Fig. 1). In eastern Alaska, moose became abundant only after predator control that reduced wolves and grizzly and black bears. Following the cessation of that control, moose rapidly declined to low densities and remained there. Our recent work shows that predation by grizzly bears and wolves maintains moose at approximately 100 moose/1,000 square kilometers.

Moose in central Alaska followed the same pattern, except that following the low-density period during the mid-1970's we again reduced the number of wolves and moose increased (Fig. 1). So, we
can characterize moose populations as commonly fluctuating at low densities relative to their food resources except following predator control.

Fig. 1. The relative numbers of moose in eastern and central Alaska from 1900 to 1988.

2. Numbers of caribou in Alaskan herds fluctuate widely and have periods of scarcity (Skoog 1968; Haber 1977). For example, the Denali herd, which lives primarily in Denali National Park, rapidly declined from about 30,000 to about 1,500 caribou by the early 1970's (Fig. 2, Haber 1977; Singer 1987). The herd has remained small for the past 15 years, and though it is increasing, it will likely be small 10 years from now. National Park Service studies indicate predation is an important source of mortality and retards population growth (Adams et al. 1987).
3. Deer in coastal southeast Alaska fluctuate with weather and predation (Merriam 1970; Olson 1979). While there was predator control, deer fluctuated fairly synchronously on islands with and without wolves (Fig. 3), although peak densities may not have been as high where wolves were present. But with the cessation of predator control in 1960, deer populations did not rebound from the severe winters of the late 1960's and early 1970's on some islands with wolves, and recovery has been delayed on other islands with wolves (Smith 1987; M. Kirchhoff and K. Pitcher, unpubl. data). Where wolves were absent, deer populations rapidly rebounded and are now at high densities. Wolves declined in abundance with the reduction in prey (Fig. 3).

Fig. 3. The trends in deer and wolf abundance on islands with wolves present (solid lines) in southeast Alaska, and the trend in deer abundance on nearby islands without wolves (dotted lines).
These examples show that, at times, unmanaged systems have low prey and predator densities. Low-density populations provide little recreation, food, or spiritual use. Sometimes predation is a major cause of prolonged prey scarcity.

**HOW DO TWO OR THREE PREDATOR SPECIES MAINTAIN STRONG CONTROL OVER PREY POPULATIONS?**

I will point out 3 of the ways predators cause prey populations to decline and/or remain at low densities.

1. Predators can kill a large proportion of the population annually. For example, Fig. 4 shows the number of moose dying from various causes in a low-density moose population in eastern Alaska. A population of 1,000 adults and yearlings produces about 670 calves, most of which die from predation. Predation is also the most important cause of mortality for adults and yearlings, followed by hunting and miscellaneous causes. By summing all the deaths in the population, we find that predators killed about one-third of the population annually. Other natural causes killed about 5% of the population, and hunters killed about 2%. Clearly, predation is a powerful force on the population.

![Diagram](image)

Fig. 4. The approximate numbers of moose dying from specific causes in a low-density moose population in eastern Alaska.

2. Mortality from predation is largely added to other sources of mortality when prey have abundant food resources. Predation does not simply replace other forms of mortality by taking animals that are about to die. Predators kill many animals that would have lived and reproduced. Predator reduction experiments demonstrate this. Survival of moose and caribou markedly improved following wolf control (Table 1).
Table 1. The percentage of moose and caribou surviving annually when wolves were abundant before wolf control and when wolves were scarce after wolf control in central Alaska during the 1970's (Gasaway et al. 1983).

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<th>Annual percent survival</th>
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<td></td>
<td>Wolves abundant</td>
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<td>Calf moose</td>
<td>15</td>
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<tr>
<td>Adult moose</td>
<td>80</td>
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<td>Calf caribou</td>
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This increased survival resulted in population growth of moose and caribou (Fig. 5). Wolves also increased when we stopped control; now predators and prey are abundant.

Fig. 5. The approximate numbers of moose, caribou, and wolves in a central Alaska management area (Game Management Unit 20A; updated from Gasaway et al. 1983). Open arrows indicate moderately severe winters and solid arrows indicate very severe winters.
Predation often results in additive mortality on the prey population—reduce that mortality and the prey population will increase at a faster rate.

3. The last point is that predators and predation do not rapidly decline as prey decline; predators lag behind their prey. For example, in our eastern Alaska study, the decline in wolf numbers lagged behind the rapid decline in moose and caribou numbers from the mid-1960's through the mid-1970's (Fig. 6). Wolves remained abundant until both moose and caribou declined to low numbers. Other examples exist in Alaska and on Isle Royale.

Fig. 6. The approximate numbers of moose, caribou, grizzly bears, and wolves in an eastern Alaska management area (Game Management Unit 20E) (Gasaway et al. 1988).
Unlike wolves, bears can remain abundant long after ungulate prey decline to low densities. Bears are not dependent on moose and caribou, as are wolves. Instead, bears rely a lot on vegetation. However, the impact of bear predation can be high on low-density prey populations because grizzlies can maintain a high kill rate even when prey are scarce. Data from 2 studies in Alaska demonstrate this point. Radio-collared grizzlies killed 1 moose calf per 7 days during spring where moose calves were scarce and killed at the same or slightly lower rate (1 calf per 8-12 days) where calves were several times more abundant (Ballard et al., in press; Boertje et al., in press).

To summarize, predators sometimes cause prey populations to decline or remain at low densities because (1) predators kill a high percentage of the population; (2) mortality from predation is partly additive, that is, it does not fully substitute for mortality from other causes; and (3) predation persists at high rates during and after prey decline.

MANAGEMENT LESSONS FOR COMPLEX PREDATOR-PREY SYSTEMS

In this section I will discuss some of the important management lessons we have learned in Alaska.

1. Do not let prey decline to low densities before deciding to manage if moderate use of wildlife is a goal. Procrastinating may cause prolonged low prey and wolf densities and little wildlife use. Some of the management problems that intensify as prey decline are:

A. The effects of predation on low-density, declining prey populations may increase on the short term. Wolves can remain abundant during the prey decline, and bears may become the major predator at low prey densities. To increase moose populations, for example, predator numbers may have to be severely depressed and both bears and wolves may have to be killed.

B. Wolves will eventually become scarce when prey decline to low densities. For example, with low prey densities in Denali National Park, wolves number only about 5 per 1,000 square km (Singer and Dalle-Molle 1985). Dave Mech told me that wolves are having a difficult time making a living in the low prey environment, based on his wolf study in Denali. In contrast, wolf density is nearly 3 times greater (13-15 per 1,000 square km) in an adjacent managed area with abundant prey. There, we reduced wolf numbers from 1976 to 1981; the low wolf density during the control period was similar to the present wolf density in Denali National Park. Thus, wolves can be fairly abundant in managed areas.
C. Recovery of low-density prey populations may require many years and intense, long-term predator control. For example, moose in eastern Alaska have been scarce (about 100 per 1,000 square km) for nearly 15 years (Fig. 7). Today, if we alter the system enough to get a 5% annual increase, moose would still be scarce 15 years from now. That is 30 years at low moose densities—a long time in a person's life, though short on an evolutionary scale. Rapidly raising moose densities to where moose are common or abundant requires about a 20% annual growth rate or a population doubling time of about 4 years (Fig. 7). That almost certainly requires a severe, prolonged predator control program, which we all want to avoid. Therefore, consider managing predator-prey systems while prey are still common.

![Fig. 7](image-url)

Fig. 7. When starting at a low moose density, many years are required for moose to become common or abundant unless the annual rate of increase is near 20%. Moose density is shown for 5%, 10%, and 20% annual rates of increase starting at year 15.

D. The last point is that wildlife helps preserve wildlife habitat and wilderness. By this I mean scarcity of wildlife opens the door to competing forms of land use. Abundant wildlife and its use can be a strong bargaining chip when arguing for rational timber, agricultural, and industrial development and retention of wildlife habitat. For example, during the early 1970's, the presence of 300,000 caribou altered oil development in Alaska's arctic. Had only a few
thousand been present at that time, development of the oil field and pipeline probably would not have accommodated wildlife as well. Today there is an intense debate over extracting oil in the Arctic National Wildlife Refuge, the calving area for the Porcupine caribou herd. Those 180,000 caribou are the major bargaining chip for retaining it as wilderness.

Other examples occur in southeast Alaska where deer are central in the argument for retaining old-growth forest, essential habitat for many wildlife species. When deer become scarce our wildlife agency has more difficulty arguing to maintain old-growth forest. I am sure it is the same in British Columbia.

2. On the long-term, prey and wolves will not remain abundant in the absence of long-term management. In other words, there is no long-term high equilibrium in some predator-prey systems. Moose in eastern Alaska serve as an example (Fig. 2 and 6). Moose increased to high densities following predator control, thus giving the system the opportunity to establish a high equilibrium. However, moose, caribou, and eventually wolves declined to a low density. Moose density is now about 100 per 1,000 square km, a very low density. Our studies show predation prevents moose numbers from increasing. This pattern of increase and decline occurred in much of interior Alaska, in hunted and unhunted areas. Therefore, long-term management is required in some areas to maintain wildlife at moderate densities.

3. Numerically, wolf populations recover rapidly from predator control. Data presented by John Elliott at this symposium showed recovery periods of 2 to 3 years in British Columbia. In Alaska, wolf populations usually recover in 3-6 years. However, socially, wolf populations are highly disrupted by predator control; social recovery probably takes much longer than numerical recovery.

4. Predator reductions have worked effectively to manage complex predator-prey systems in Alaska. Benefits have been increased prey, wolves, and recreation. For example, wolves, moose, and caribou are at low densities in Denali National Park compared with an adjacent management area where predator numbers were periodically reduced (Fig. 5). As previously mentioned, wolves in the managed area are now about 3 times the density in Denali Park. Earlier today, Dale Seip suggested it may be possible to raise long-term wolf densities if prey numbers are increased through wolf control. This clearly can be done and is being done in parts of Alaska. Increasing wolf abundance is a goal in portions of Alaska. The wolf is a highly valued species.

Reducing predation through lethal predator control programs is unpopular to the majority of people and is divisive. Hence, we are investigating new, nonlethal means of manipulating predator-prey systems in more socially acceptable ways. Several alternatives hold promise.
5. The last lesson is to allocate shares of prey to predators and man in written management plans. This assures people that predators have a long-term place in the ecosystem and shows how man, wolves, and bears will share prey. The flow chart in Figure 4, for example, quickly shows all concerned how the moose resource is shared in a portion of eastern Alaska. There is no mistaking that bears and wolves are allocated most of the moose resource; one-third to predators and 2% to man. A flow chart such as this helps clarify current or future allocation decisions.

CONCLUSION

I will conclude with 4 points.

1. Predator-prey management is necessary in many systems to sustain the long-term desires of people. The reason—natural processes sometimes cause wolves and their prey to become scarce for long periods. Low wildlife densities provide for little use. If predator-prey systems commonly remained at a high equilibrium, then we could manipulate them and forget about intensive management for decades. That doesn't seem to be the case.

2. Do not wait until prey are at low densities to begin managing predator-prey systems. Recovery of prey and wolf populations can take a long time and require severe management actions.

3. Predators can be abundant in exploited systems. I have given you examples in Alaska. Man can share prey with large predators without driving predators to prolonged low densities.

4. Lastly, I want to stress that abundant wildlife helps preserve wilderness and large carnivores. By maintaining fairly abundant wildlife, we can more effectively argue for preserving wildlife habitat, and especially wilderness. Without wilderness, few wolves and grizzlies will survive.

Management of large carnivores has become a battle ground among conservationists. We have become so polarized that we no longer stand together on the more important issues. It is time to unite! It is time to respect our ethical differences regarding wildlife use and get on with ensuring a long-term place for wildlife in North America.

Let's not give our wildlife habitat to industry, agriculture, and urban sprawl because we temporally let our large ungulates and carnivores decline to low densities and lose their competitive value in the race for land uses.

If we can preserve the ungulate-carnivore systems and the wilderness they require, then there will be plenty of wildlife for viewing, hunting, and spiritual use.
LITERATURE CITED


