

# The effects of wolf predation



Abstract: This paper discusses four hypotheses to explain the effects of wolf predation on prey populations of large ungulates. The four proposed hypotheses examined are the predation limiting hypothesis, the predation regulating hypothesis, the predator pit hypothesis, and the stable limit cycle hypothesis. There is much research literature that discusses how these hypotheses can be used to interpret various data sets obtained from field studies. It was concluded that the predation limiting hypothesis fit most study cases, but that more research is necessary to account for multiple predator - multiple prey relationships.

The effects of predation can have an enormous impact on the ecological organization and structure of communities. The processes of predation affect virtually every species to some degree or another. Predation can be defined as when members of one species eat (and/or kill) those of another species. The specific type of predation between wolves and large ungulates involves carnivores preying on herbivores. Predation can have many possible effects on the interrelations of populations. To draw any correlations between the effects of these predator-prey interactions requires studies of a long duration, and statistical

analysis of large data sets representative of the populations as a whole. Predation could limit the prey distribution and decrease abundance. Such limitation may be desirable in the case of pest species, or undesirable to some individuals as with game animals or endangered species. Predation may also act as a major selective force. The effects of predator prey coevolution can explain many evolutionary adaptations in both predator and prey species.

The effects of wolf predation on species of large ungulates have proven to be controversial and elusive. There have been many different models proposed to describe the processes operating on populations influenced by wolf predation. Some of the proposed mechanisms include the predation limiting hypothesis, the predation regulating hypothesis, the predator pit hypothesis, and the stable limit cycle hypothesis (Boutin 1992). The purpose of this paper is to assess the empirical data on population dynamics and attempt to determine if one of the four hypotheses is a better model of the effects of wolf predation on ungulate population densities.

The predation limiting hypothesis proposes that predation is the primary factor that limits prey density. In this non-equilibrium model recurrent fluctuations occur in the prey population. This implies that the prey population does not return to some particular equilibrium after deviation.

The predation limiting hypothesis involves a density independent mechanism. The mechanism might apply to one prey - one predator systems (Boutin 1992). This hypothesis predicts that losses of prey due to predation will be large enough to halt prey population increase.

Many studies support the hypothesis that predation limits prey density.

Bergerud et al. (1983) concluded from their study of the interrelations of wolves and moose in the Pukaskwa National Park that wolf predation limited, and may have caused a decline in, the moose population, and that if wolves were eliminated, the moose population would increase until limited by some other regulatory factor, such as food availability. However, they go on to point out that this upper limit will not be sustainable, but will eventually lead to

resource depletion and population decline. Seip (1992) found that high wolf predation

on caribou in the Quesnel Lake area resulted in a decline in the population, while low wolf predation in the Wells Gray Provincial Park resulted in a slowly increasing population. Wolf predation at the Quesnel Lake area remained high despite a fifty percent decline in the caribou population, indicating that mortality due to predation was not density-dependent within this range of population densities. Dale et al. (1994), in their study of wolves and caribou in Gates National Park and Preserve, showed that wolf predation can be an important limiting factor at low caribou population densities, and may have an anti-regulatory effect. They also state that wolf predation may affect the distribution and abundance of caribou populations.

Bergerud and Ballard (1988), in their interpretation of the Nelchina caribou herd case history, said that during and immediately following a reduction in the wolf population, calf recruitment increased, which should result in a future caribou population increase. Gasaway et al. (1983) also indicated that wolf predation can sufficiently increase the rate of mortality in a prey population to prevent the population's increase. Even though there has been much support of this hypothesis, Boutin (1992) suggests that "there is little doubt that predation is a limiting factor, but in cases where its magnitude has been measured, it is no greater than other factors such as hunting."

A second hypothesis about the effects of wolf predation is the predation regulating hypothesis, which proposes that predation regulates prey densities around a low-density equilibrium. This hypothesis fits an

equilibrium model, and assumes that following deviation, prey populations return to their pre-existing equilibrium levels. This predator regulating hypothesis proposes that predation is a density-dependent mechanism affecting low to intermediate prey densities, and a density-independent mechanism at high prey densities.

Some research supports predation as a regulating mechanism. Messier (1985), in a study of moose near Quebec, Canada, draws the conclusion that wolf-ungulate systems, if regulated naturally, stabilize at low prey and low predator population densities. In Messier's (1994) later analysis, based on twenty-seven studies where moose were the dominant prey species of wolves, he determined that wolf predation can be density-dependent at the lower range of moose densities. This result demonstrates that predation is capable of regulating ungulate populations. Even so, according to Boutin (1992) more studies are necessary, particularly at high moose densities, to determine if predation is regulatory.

A third proposal to model the effects of wolf predation on prey populations is the predator pit hypothesis. This hypothesis is a multiple equilibria model. It proposes that predation regulates prey densities around a low-density equilibrium. The prey population can then escape this regulation once prey densities pass a certain threshold. Once this takes place, the population reaches an upper equilibrium.

At this upper equilibrium, the prey population densities are regulated by competition for (and or availability of) food. This predator pit hypothesis assumes that predator losses are density-dependent at low prey densities,

but inversely density-dependent at high prey densities. Van Ballenberghe (1985) states that wolf population regulation is needed when a caribou herd population declines and becomes trapped in a predator pit, wherein predators are able to prevent caribou populations from increasing.

The final model that attempts to describe the effects of predation on prey populations is the stable limit cycle hypothesis. This hypothesis proposes that vulnerability of prey to predation depends on past environmental conditions. According to this theory, individuals of a prey population born under unfavorable conditions are more vulnerable to predation throughout their adult lives than those born under favorable conditions.

This model would produce time lags between the proliferation of the predator and the prey populations, in effect generating recurring cycles. Boutin (1992) states that if this hypothesis is correct, the effects of food availability (or the lack of) should be more subtle than outright starvation. Relatively severe winters could have long-term effects by altering growth, production, and vulnerability. Thompson and Peterson (1988) reported that there are no documented cases of wolf predation imposing a long-term limit on ungulate populations independent of environmental influences. They also point out that summer moose calf mortality was high whether predators were present or not, and that snow conditions during the winter affected the vulnerability of calves to predation. Messier (1994) asserts that snow accumulation during consecutive winters does not create a cumulative impact on the nutritional status of deer and moose.

All of the four proposed theories mentioned above could describe the interrelationships between the predation of wolves and their usual north american prey of large ungulate species. There has been ample evidence presented in the primary research literature to support any one of the four potential models. The predation limiting hypothesis seems to enjoy wide popular support, and seems to most accurately describe most of the trends observed in predator-prey populations.

Most researchers seem to think that more specific studies need to be conducted to find an ideal model of the effects of predation. Bergerud and Ballard (1988) stated " A simple numbers argument regarding prey: predator ratios overlooks the complexities in multi-predator-prey systems that can involve surplus killing, additive predation between predators, enhancement and interference between predator species, switch over between prey species, and a three-fold variation in food consumption rates by wolves." Dale et al. (1994) stated that further knowledge of the factors affecting prey switching, such as density-dependent changes in vulnerability within and between prey species, and further knowledge of wolf population response is needed to

draw any firm conclusions. Boutin (1992) also proposed that the full impact of predation has seldom been measured because researchers have concentrated on measuring losses of prey to wolves only. Recently, bear predation on moose calves has been found to be substantial, but there are few studies which examine this phenomenon (Boutin 1992). Messier (1994) also pointed out that grizzly and black bears may be important predators of moose calves during the summer. Seip (1992), too, states that bear

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predation was a significant cause of adult caribou mortality. These points emphasize that multiple-predator and multiple-prey systems are probably at work in the natural environment, and we must not over generalize a one predator - one prey hypothesis in the attempt to interpret the overall trends of the effects of predation of wolves on large ungulate populations.