Mini-Review

Trophic Interactions of Gray Wolves (*Canis lupus*), the Keystone Species in Yellowstone National Park

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Abstract

The gray wolf (Canis lupus) is an apex predator described as a keystone species in Yellowstone National Park. Their importance in this habitat was unknown until they were anthropogenically extirpated in the 1920s. The 75-year absence of gray wolves in Yellowstone led to declines in biodiversity, and habitat quality, all of which is gradually returning upon wolf reintroduction in 1995. Trophic interactions are the driving forces behind the gray wolves' ability to directly and indirectly provide benefits for almost all species of fauna and flora within Yellowstone National Park. This paper reviews how wolves' trophic interactions have helped in reshaping the dynamics of Yellowstone National Park.

Keywords: Gray Wolf, Apex Predator, Keystone Species, Trophic Cascade, Trophic Interaction

pecies diversity comes in many forms yet varies between habitats. Few species have the ability to significantly alter or affect (both directly and indirectly) the environment in which they live¹. These organisms are known as keystone species and through their presence or absence they have an impact on biodiversity, species richness, and the landscape and niches they occupy². Keystone species' effects and interactions within the environment are exponentially greater than their population size³. Keystone species are most often predatory animals able to maintain stable population sizes of lower trophic levels, which leads to increases in biodiversity and changes in resource abundance and distribution. Without these species, the habitats they maintain would be radically different or nonexistent, and ecosystem productivity and biodiversity would decline⁴.

Gray wolf (*Canis lupus*) of Yellowstone National Park are a prime example of an organism that is considered to be a keystone species. Through their trophic interactions and their status as an apex predator, wolves are able to both successfully limit populations of large herbivorous animals and force behavioural changes on smaller carnivores, such as avoidance and altered foraging/hunting strategies¹.

Yellowstone National Park (Yellowstone) is an 8992 sq. km wilderness recreational park located on the state borders of Wyoming, Montana and Idaho, USA. It was established in 1872 making it the world's first national park². The forests and meadows of this pristine habitat provide shelter and food for the species that inhabit Yellowstone⁵. Some of the more famous species of the park are the carnivorous, predatory mammals like gray wolves and coyotes (*Canis latrans*), the omnivorous grizzly bear (*Ursus arctos horribilis*), and herbivores like elk (*Cervus canadensis*) and beaver (*Castor canadensis*). The balance of predator-to-prey animals is critical for ecosystem productivity and Yellowstone is a testament to the significant role of gray wolves in the park².

Prior to the early 20th century, wolves were an integral part of Yellowstone. As settlement began in the early 1800s, the fear of wolves preying on livestock resulted in a cull and subsequent extirpation by the 1920s². The extirpation resulted in major ecosystem changes through the loss of trophic interactions in a top-down trophic cascade¹. A trophic cascade occurs when an apex predator, such as the wolf, changes the behaviour of their prey, the elk in this case, through population reduction and decreased foraging time, releasing plant species from foraging pressure and allowing them to recover. This cascade had great effects on species such as the elk, grizzly bears, and beavers as well as habitat quality^{6, 2}. With the absence of the wolves, elk overgrazed on plants such as the willow (Salix spp.) stands along riparian systems, causing a decrease in available food for grizzly bears and beavers^{7, 2}. The loss of plants and root structures along the riparian system resulted in sediment erosion along the banks. This led to further loss of plant diversity and the widening and change of river flow^{7, 2}.

Wolves were reintroduced into Yellowstone after a comprehensive environmental impact assessment looked at the possible implications⁶. Wolf reintroduction took place in 1995 and 1996⁷, with 31 wolves coming from Canada. The population quickly grew to 270 by the end of 2002¹. As the various wolf packs settled into their new environment, a change in Yellowstone's habitat slowly emerged. Their ecological importance as a keystone species was becoming more



apparent as the habitat slowly returned to a pre-wolf extirpation state. Willow stands along the riparian zones were reestablishing, beavers and grizzly bears were returning to their native home range, and elk and coyote foraging behaviour were changing^{6, 2}.

As wolves expanded their territorial range within Yellowstone, a change was observed in the foraging behaviour of the resident elk population¹. Elk decreased their foraging time on plants such as willow, aspen (*Populus tremuloides*), and cottonwood (*Populus angustifolia*) as they became more vigilant of wolf predation^{2, 8}. With this increase in awareness of their surroundings and decreased foraging pressure, a recovery of plants began in the region.

Elk were wolves' primary prey within Yellowstone as they had a high abundance and pack cohesion made them easily obtainable^{2, 1}. The increased predation on elk has slowly resulted in the suppression of elk as well as their foraging habitats. This has had a compounding effect on plants, allowing regrowth and reshaping of the environment^{2, 1, 8}.

As an apex predator, wolves interact with all trophic levels directly or indirectly⁹. Indirectly, they interact with the grizzly bear that is also considered an apex predator, but in the sense that it is an omnivore⁸. Prior to wolf reintroduction, grizzly bear populations were affected by the overgrazing of plant biomass by elk populations^{2, 8}. In spring after hibernation, grizzly bears need easily obtainable calories usually in the form of insects, carrion, and vegetative material, including berries and grasses⁸. The overgrazing by elk reduces plant biomass available to the bears and also reduces cover required later in the season for safe foraging⁸.

In fall, grizzly bears enter a period of hyperphagia where they need to store enough energy from carbohydrate rich foods for hibernation⁸. This time is especially critical for female bears as they gestate, give birth, and lactate while hibernating. Wolves have an indirect relationship with the grizzly bears by directly reducing the elk population that overgraze on essential plants needed by the bears^{2, 8, 10}. The wolves also provide carrion left behind at their kill sites that grizzly bears scavenge off of with low energetic costs, providing some of the essential calories for winter survival^{2, 8}.

The removal of wolves from their ecosystem negatively affected the conservation of the fauna and flora in the region. The riparian systems; ungulate, beaver, and grizzly bear populations; and mesopredators (coyotes) were all impacted, causing a trophic cascade^{2, 1, 8}. The removal of apex predators can also result in a mesopredator release, where a smaller predator such as the coyote is suppressed by a larger predator no longer has that inhibiting effect¹¹.

Wolves have the ability to change the behaviour of the animals they interact with based on their predatory status. In the presence of wolves¹, coyotes changed their behaviour and foraging habits to avoid areas populated with wolves and their dens. These dens were previously used as hunting grounds for coyotes after the wolves were extirpated from Yellowstone in the early 20th century¹. After wolves were reintroduced, coyotes were deterred from foraging near the wolf dens as the new wolf packs reclaimed these denning areas for themselves¹. An inverse relationship was also observed between coyotes and small mammals inhabiting areas near wolf dens: as coyote populations decreased, small mammal populations increased. This correlation appears to happen because coyotes would prey upon small mammals, and as wolves gradually reclaimed their old territory pushing the coyotes further out, the small mammals moved back toward the dens because of less predation pressure¹.

Through trophic interactions with other trophic levels and their ability to alter animal behaviour, wolves play an integral part in their habitat. Their profound effects they have on the ecosystem of Yellowstone have been shown through studies and numerous ecosystem changes. With these changes that are already apparent, it warrants further investigation down the line to continue observations of Yellowstone and how this ecosystem continues to recover from a time of absence with wolves.

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