Life and behaviour of wolves: Predation risk and the structure of ecosystems

Since the re-introduction of wolves into Yellowstone the influence of wolf predation on ungulates and the consequent effects this has upon vegetation communities has come to light. These knock-on effects caused by the actions of one population promoting changes through multiple levels of the food web are known as trophic cascades.

Pete Haswell reports

By preventing overpopulation of ungulates, wolf predation averts a wealth of potentially negative interactions that overgrazing/browsing by herbivores can lead to. Through the reduction of ungulate pressure on riverside vegetation, bank stability is maintained and flooding prevented, habitat for pest-controlling birds and pollinating insects as well as shady fish nurseries are all maintained. Some grassy herbaceous areas are permitted to advance to forest and carcasses provide food for scavengers in hard winters. A wealth of valuable ecosystem services are all maintained in balance by the predatory acts of carnivores. But is it predatory action on population size alone that has this top down influence or is there more to it?

The activity patterns that animals exhibit are a complex compromise between optimal foraging, social activities and environmental constraints. Ungulates like all other mammals spend their days tending to their immediate biological requirements and welfare, with temperature regulation and the need for food and water being on top of the list. They also spend time interacting socially and attempting to fulfill life-cycle needs such as learning, play and reproduction. In some ungulate species such as red deer this can involve massive energy expenditure during the breeding season or rut that leaves little room for alternative activity.

An animal balances its needs against environmental constraints. One such factor is the avoidance of pests or parasites. Deer are known to exhibit variation in their use of and preference for certain altitudes during the summer months when midges and other blood sucking insects are plentiful and adapt their daily grazing routine to avoid these pests. Wild boars among others wallow in an attempt to reduce pest irritation. So if ungulates deviate from optimal foraging and social requirements to invest time avoiding irritation and degradation from pests, surely they must exhibit similar habitat preferences and alterations in behaviour to avoid predation? The need to survive clearly represents the most imperative environmental constraint on their ability to conduct other activities.

PREY SPECIES EXHIBIT NUMEROUS BEHAVIOURAL RESPONSES TO PREDATION RISK:

Changes in group size, reduced movement, increased vigilance, reduced foraging and habitat selectivity. The associated focus of foraging pressure accompanying these behavioural responses is likely to impact vegetation community structure on a local scale. On a larger scale ungulate habitat selection and the associated grazing/browsing pressure is likely to be important in shaping vegetation communities at the ecosystem level.

Habitat selection reflects a balance between loss of fitness due to predation risk and fitness gain due to improved forage access. Risk-driven alterations in habitat use by prey can alter population and community dynamics in several ways. Constraints on habitat selection may carry fitness costs that reduce prey numbers beyond the effects of predation itself. Changes in prey behaviour may alter their impacts on vegetation resources even if numbers remain constant.

Terrain fear (predation-risk effects associated with encounter and escape situations) has influence on habitat use by herbivorous prey species. Elk avoid areas offering poor visibility or those with obstacles that make escape difficult. In areas of high wolf presence they increasingly select to forage at sites that allow early detection and successful escape from wolves. Elk do not avoid travel in high wolf-use areas but show spatial avoidance and a switch in habitat preferences when doing so.

Wolves tend to travel along riparian (riverside) areas and do not opt to travel in coniferous forest. elk movements may reflect avoidance in response to wolf travel routes and signs of predator presence as they show preference for routes offering coniferous forest cover when travelling in areas with high wolf activity. Some studies show wolf kills to be significantly more likely in grassland areas far from woodland edges in comparison with sites close to woodland. It is suggested that elk move to forest edges when risk is detected. Although elk prefer to forage on aspen, studies have indicated they move away from riparian aspen stands or those at forest edges and into coniferous forest when wolf use of an area is high.

In response to predation risk, female elk show stronger preference to wooded areas than stags. It seems males are less capable of paying the costs of anti-predator behaviour. In winter they are in worse physical condition due to weight lost during the rut and significantly lower bone marrow fat stores caused by malnutrition. They also travel in smaller groups, offering less assistance in watching for predators reducing time spent foraging.

Clearly there is variation among species and ecosystems in the way habitat features affect risk and equally how behaviour is adjusted in response to risk. Nonetheless the impact of predator activity can clearly lead to the establishment of prey and plant refuge areas. Ungulate populations can structure plant communities through patterns of movement and foraging decisions. Reduced grazing/ browsing pressure in areas of high predation risk
will impact vegetation structure and diversity. If elk densities became low enough, then a more widespread release from browsing of woody plants would be expected. However, observations indicate release of pressure on vegetation at high risk sites only. Lack of wolf presence results in unimpeded grazing and simpler less diverse plant communities. Elk habitat preference in high wolf use areas results in decreased use of some aspen and increased use of conifer forests. This lower grazing pressure allows the sustainment of aspen and the progression of vegetation communities eventually resulting in tree cover.

LITTLE IS KNOWN ABOUT HOW UNGULATES USE SCENT AND SOUND IN COMBINATION WITH VISUAL INDICATORS TO EVALUATE PREDATION RISK. However, elk are known to use predator cues to directly assess local risk on short time scales rather than by location alone. It is important to consider variation in risk over time when assessing anti-predator habitat selection by prey. Predation risk varies in space and time due to wolf movements, colonisation and pack failure. Persistence of grazing limited plant refuge sites and the related increase in plant biomass and progression to woody vegetation relies on stability of wolf presence. Changes in level of wolf use on the landscape would alter patterns of refuge and the accompanying vegetation structure. Reduced foraging pressure in one area should be in general mirrored by increased pressure in another. It is highly plausible that through impacts upon herbivore movement and foraging behaviour, wolf activity helps maintain a mosaic of habitat types with varied plant communities providing a constantly changing yet variable landscape.

We do still need to be aware of impacts other biotic factors have such as forage availability or the effects human activity have on herbivore habitat use. Elk and wolves both avoid roads and other human disturbance. Natural migrations can often be interrupted by our actions. Human hunting seasons have been found to cause some animals to move out of profitable grassy meadows and into forests, returning once hunting seasons are over. This leads to a significant change of diet and time spent browsing. Likewise environmental factors such as snow depth should be considered. Snow depth limits habitat selection for grazing, valley bottoms with less snow depth often suffer from heavily impacted riparian areas due to herbivore activity.

ALTHOUGH ELK ANTI-PREDATOR BEHAVIOUR COULD DRIVE A TROPHIC CASCADE, CHANGES IN DENSITY AND NUMBERS COULD ALSO AFFECT ELK–PLANT INTERACTIONS. Numbers and behaviour have both changed since wolf recovery in Yellowstone. There is further need to understand the interactions of lethal and non-lethal predator activity in structuring vegetation communities and ecosystems. Previous long-term population control efforts by the Yellowstone National Park Service have not been documented to have effect on winter patterns of elk behaviour. Elk populations artificially maintained from 1930-68 showed no significant effects on aspen recruitment. Nor have the actions of cougar, bear or coyotes. It appears unlikely that observed trophic cascades are purely the result of lower elk density but instead are largely behaviourally mediated. Non-lethal action of predators may have an even stronger influence on food webs than population control alone. Land management goals should clearly focus on the recovery of natural processes in order to maintain ecosystem structure and stability.

Pete Haswell

Pete Haswell, BSc Hons Environmental Science (Biodiversity and Conservation), is collaborating with Josip Kusak on a project the UKWCT supports in Croatia. You can read more about his work on his website http://petehaswellwolfforschung.wordpress.com/