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Howling About Trophic Cascades

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Abstract Following evolutionary theory and an agriculture model, ecosystem research has stressed bottom-up dynamics, implying that top wild predators are epiphenomenal effects of more basic causes. As such, they are assumed expendable. A more modern co-evolutionary and wilderness approach — trophic cascades — instead suggests that top predators, whose effects flow down to fundamental biological processes, are co-equal causes of ecosystem health. Their survival, then, should be supported. This article, based on extensive research including the author's participation in a major field project, provides informational resources for teaching trophic cascades, using wolves as a case study. As charismatic, iconic, thriving but still endangered, well-studied, and terrestrial carnivores, wolves are ideal for enlightening students about what otherwise might be dry abstractions about crucial ecosystem processes. The article ends with student exercises and broader lessons for environmental education.

When the wolves move, everything moves.

Anonymous tracker to the author.

What makes for a healthy ecosystem? Researchers, following evolutionary theory and an agricultural model, have traditionally stressed a bottom-up approach; namely, that sunlight, water, and soil nutrients serve the needs of seeds that produce plants, which in turn feed herbivores and other life forms, which in turn feed carnivores. This system displays dynamic equilibrium; for example, if herbivores eat too much of the available plant food, malnutrition sets in and their numbers decline, letting plants reflourish, thereby allowing herbivore populations to recover. True, carnivores may reduce herbivore populations somewhat, but they have only a minor net effect on the system as a whole. This 'plant defence hypothesis' seems to imply that top predators are peripheral to ecosystem health and regulation (Murdoch, 1966; Polis, 1994). Saving endangered predators may be desirable for aesthetic and other reasons, but hardly necessary or even especially useful.

Down the Up Staircase

This bottom-up approach, however, is only part of the story. A top-down approach — trophic cascades — has recently stressed that top predators have multiple positive

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effects throughout levels of food chains, and as such are necessary for full ecosystem vitality (Beschta & Ripple, 2012; Estes et al., 2011).

Following co-evolutionary theory and a wilderness model, a growing number of researchers are stressing how organisms exert selective pressure on related others, such that they affect each other's evolution. Such a relationship often obtains between predator and prey species. For example, why do deer and wolves run so fast? The deer does not run fast just because it ate the right greenery, but because over the centuries it had to escape the fast wolf to survive (top-down effect). By the same token, the wolf has to run fast to catch the fast deer to survive (bottom-up effect). In short, their locomotion physiology has been driven by their relationship — the two species co-evolved across trophic levels.

Top predators, then, may exert major top-down effects (Ripple & Beschta, 2009). This notion, in fact, can be found throughout the ages. Ancient Chinese farmers noticed less crop damage when predators limited herbivore numbers. In the Amazon, tribalists say that if the jaguar dies, so will the people. More recently, the idea has been found in the writings of Aldo Leopold and later observers, who noted that predators limit herbivores, allowing the world to stay green — the 'Green World Hypothesis' (Eisenberg, 2008; Hairston, Smith, & Slobodkin, 1960; Ripple & Beschta, 2005).

Today's scientists are finding 'mounting evidence' of such top-down trophic cascades descending from apex predators down to the composition of soil itself (Ripple, Larsen, Renkin, & Smith, 2001, p. 232). Predator-prey effects that alter the abundance, biomass, and productivity of population communities across multiple links of a food chain are seen in simple and complex, micro and macro, and aquatic and terrestrial ecosystems. Questions about trophic cascades have shifted from whether to when, where, and how often (Beschta & Ripple, 2009; Pace, Cole, Carpenter, & Kitchell, 1999; Terborgh & Estes, 2010).

Yet debate persists. For example, uncertainty obtains about the relative importance of the two approaches — bottom-up versus top-down. For this reason, the notion has been singled out by the US National Research Council as a key area for investigation (Ripple & Beschta, 2003). As such, students can be well served by systematic and detailed instruction that offers a vivid case of trophic cascades initiated by a top predator. Further, since healthy ecosystems serve our own survival, and if a top predator helps make them healthy, then students need to know the importance of its survival.

This article offers environmental educators resources for presenting the trophic cascade notion to students using the gray wolf (*Canis lupus*) as a case study. It is based on a meta-analysis of recent scientific literature on wolves; the author's personal experience as a tracker on a major project researching the trophic cascade effects of wolf reintroduction in the Crown of the Continent Ecosystem of the North American West since 1995 (Kowalewski, 2009; *National Geographic*, 2010); conversations with longtime wolf trackers; and interviews with caretakers in commercial 'wolf sanctuaries'. The article is designed as a module for courses in ecology, ecosystem dynamics, conservation biology, endangered species, wildlife management, environmental law and politics, and related fields. As research accumulates, it may serve as a template for a course on trophic cascades in its own right.

Why the Wolf?

Environmental educators, while wishing to provide their charges with intellectual and especially scientific resources, face the daunting challenge of student interest. The following criteria, offered here to justify the wolf as a case study for teaching trophic

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cascades, can be generalised for selection of material to illustrate abstract ecosystem concepts: charisma, iconography, impending change, survival threat, adequate research, and theoretical debate.

The wolf is ideal for all these reasons. First, it is charismatic, engendering immediate fascination among students. Frequently appearing in the mass media, it ranks right at the top of the fauna charisma scale together with dinosaurs and bears for its ability to command the young's attention. Other predators that cause trophic cascades, like the sea otter, may evoke warm feelings but rarely elicit excitement and interest like the wolf.

Second, the wolf is iconic, symbolising wilderness more than any other species. Students, then, through their knowledge of the beneficial effects of wolves, can help make the future public case for preservation of wilderness more solid. In politics, symbols matter. In fact, one might argue that, for wilderness preservation, the wolf is the most important species around: As goes the iconic wolf, so goes wilderness.

Third, the species signals impending ecosystem changes for which students need to be prepared. Rebounding rapidly everywhere it has been reintroduced, the wolf will interact more and more with humans, who still have very little understanding of its behavior. Wolves are superbly equipped to survive in all types of wild habitat, at one time being found across the northern hemisphere, including every US state except Hawaii, and representing the most widely distributed carnivore there (Ripple & Beschta, 2005; Smith, Peterson, & Houston, 2003). Already coming into conflict with ranching and other interests, wolves are now legally hunted in some US western states, a controversy in itself. Since our species will certainly be dealing with a lot of wolves in the near future, their broad effects on ecosystems need to be learnt quickly lest a more severe backlash be provoked.

Fourth, the survival of the species is still threatened. Although wolves are coming back strongly, population size does not imply robustness, as we found out with such prolific species as bison and passenger pigeons. Most species, it appears, can go extinct in short order. As for the wolf, not only is it threatened by canine parvovirus, an infectious disease. Worse, no other species has been so consciously and relentlessly persecuted. When wolves howled at the moon, memories of pagans — 'witches' — celebrating nature in tune with lunar phases were evoked, sparking vicious attacks by threatened elites. Wolves were tortured, demonised, mutilated, burned alive at the stake, and almost made extinct — just like witches — with near-hysterical zeal. So many wolves were poisoned in the US West that strychnine became a verb with wolves as its direct object (Schultz, 2010). Whereas foxes and coyotes also killed livestock and pets and so were hunted and trapped, they also had certain redeeming qualities — for example, the 'sly' fox and 'wily' coyote. Indeed, the Big Bad Wolf myth persists, as seen in media attacks and illegal killings. As such, the wolf, arguably the most controversial wild species in the world, can elicit sharp debate in classrooms, an occurrence increasingly favoured by environmental education researchers (Sanera, 1998). Today, some anti-environmentalists would love to see them all dead. A current backwoods saying in the US West goes: 'Shoot, shovel, and shut up.' It is no exaggeration to say that human activity is still the wolf's worst enemy, a claim supported by science (Ballard, Whitman, & Gardner, 1987; Potvin & Jolicoeur, 1988). Many humans still feel that wolves can do no good to humans and even have it in for us, despite lack of evidence (Smith et al., 2003). Wolves, in fact, assiduously avoid areas of human concentration, preferring areas of minimal road density (Bangs, 1991; Mladenoff, Haiaght, Sickley, & Wydeven, 1997). This special animus against wolves suggests not merely a need for special protection, but also for extensive public education detailing not only how they do not threaten our survival, but even enhance it through trophic cascades.

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Fifth, the species is well studied by wildlife researchers. This article, for example, uses information from no less than 66 research articles on wolves in 26 scientific journals; in particular, *Canadian Journal of Zoology, Journal of Wildlife Management,* and *Wildlife Society Bulletin*.

Finally, the wolf, being terrestrial, serves as a case to fuel a theoretical debate. While many scientists have accepted the notion of trophic cascades for aquatic food systems, controversy about terrestrial ones remains, despite growing supportive evidence (Ripple & Beschta, 2007).

Gray Wolf, Green World

Environmental educators, well aware of the low level of science-based environmental knowledge among the public and students, need such up-to-date information themselves. Yet because of many other tasks, they face high information costs. As such, 'ecological literacy' among teachers themselves is often low (Cutter-Mackenzie & Smith, 2003). The temptation, then, is to fall back on sentimental reasons for saving ecosystems, thereby inviting attack for indoctrinating instead of educating (Sanera, 1998). Ecological illiteracy also leaves the field open to unscientific disinformation by anti-environmentalists. Not only can scientific information be an influential factor in developing public knowledge about complex environmental issues (Rickinson, 2001), it is an important and necessary factor in determining environmental behavior (Robelia & Murphy, 2012). The following detailed description, then, modelled for presentation to students, can serve as a useful informational resource for teachers.

In overview, carnivores have density effects on herbivores and other species (e.g., reducing their numbers via predation) and behavioural effects (e.g., altering their feeding patterns). These effects cascade down to further impacts on vegetative health, herbivore and scavenger densities, bird abundance and diversity, and soil nutrients. As such, top carnivores can benefit the entire life support system of humans. Further, they have net beneficial effects on economies, recreational opportunities, and other human networks.

Density effects are direct and indirect. Direct effects are immediate reductions of herbivores via predation. The largest such wolf effects are on ungulates, specifically elk, deer, and moose. But no evidence can be found that wolves drive these prey numbers down anywhere close to endangerment. In fact, studies repeatedly show that when ungulate prey numbers decline from wolf kills, wolves easily switch to other prey, such as beavers and hares (Forbes & Theberge, 1996).

Wolves also have density effects on mesocarnivores, such as otters and martens. Yet the most dramatic effect is on coyotes, whose populations fall precipitously (Arjo, Pletscher, & Ream, 2002). Wolves are downright antipathetic to coyotes, much like African lions to hyenas. Indeed, only three years after wolf reintroduction into Yellowstone National Park, coyote numbers fell by no less than half (NRDC, 2009; Smith et al., 2003). Perhaps for good reason, when wolves enter the scene, coyotes, for self-defence, reduce the size of their den entryways and shift from a solitude and pairing pattern to one of pairs and large packs (author's interviews with wolf trackers).

Wolves also change the behaviours of their herbivore prey. Elk, for example, move around more and change their habitat use, shifting from thick aspen groves and riparian areas, where wolves prefer to hunt during most of the year, to more open areas and conifer forests for better detection of wolves and quicker escape, thereby allowing the deciduous trees a reprieve from browsing (Fortin et al., 2005; Kunkel & Pletscher, 2001; Ripple & Beschta, 2003, 2004). As well, they look up more often from browsing when wolves are around, again resulting in less heavy damage to trees (Ripple & Larsen, 2000). Moose and bison, too, become more vigilant and responsive to bird alarms,

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causing them to feed less heavily on vegetation (Berger, 1999; Laundre, Hernandez, L, & Altendorf, 2001).

Because of these density and behavioural effects on ungulates, herbivory is curtailed and so vegetation thrives when wolves are around (Berger, Stacey, Bellis, & Johnson, 2001). In terms of species diversity, age structure, production recruitment, height, disease, and spatial distribution, the world becomes 'greener' (Ripple & Beschta, 2003, 2004, 2005; Ripple & Larsen, 2000; Ripple et al., 2001). Browse intensity on aspen, cottonwood, and willow, as measured for example by per cent of leaders fed upon, is reduced (Hebblewhite et al., 2005; Laundre et al., 2001; Ripple & Beschta, 2007; Smith et al., 2003), while cottonwood and aspen recruitment rises (Beschta, 2005; Beschta & Ripple, 2007).

Lest one feel sorry for the herbivores, research has found that, without the wolf, when herbivore populations explode and vegetation starts to decline as a result, their numbers quickly face hard times in terms of starvation and disease and so can easily crash. Wolves, then, can be said to prevent herbivores from overshooting their food supply (Peterson, 1999).

Further, since the coyote feeds heavily on the newborns of ungulates, its reduction by the wolf in fact prevents their populations from crashing; and indeed, in the case of pronghorns, promotes a population increase for a species in decline in some regions (Ripple & Beschta, 2005). Other herbivores also benefit. Since the prime food and construction materials of beavers in riparian areas, such as cottonwood and willow, rebound when wolves are around, the number of beaver lodges shows a marked increase (Hebblewhite et al., 2005; Ripple & Beschta, 2003, 2004). At the same time, the wolf feeds on beavers in the non-winter months, preventing their populations from overshooting (Forbes & Theberge, 1996; Nelson & Mech, 1992).

Other carnivores — in particular, scavengers — also benefit. Wolf-killed carcasses feed up to 15 species, including magpies and threatened species like grizzlies and eagles (Ripple & Beschta, 2005). This contribution by wolves is especially important in an era of global warming, which reduces the number of winter-killed carcasses and thus food for scavengers (Smith et al., 2003).

Birds are special beneficiaries in terms of abundance and diversity. Songbirds in riparian areas thrive when wolves are around (Hebblewhite et al., 2005). The recovery of vegetation allows bud-, berry-, and seed-eating bird populations to rise. Since the coyote feeds heavily on small rodents, then as the wolf reduces its numbers, predatory birds like eagles and hawks find more abundant food. The rise of beaver populations promotes wetland areas, hotspots of biodiversity, hosting fish and other creatures that herons and other aquatic birds can feed upon (Ripple & Beschta, 2004).

Soil, too, benefits. As deciduous trees recover, more leaf litter covers the ground, promoting rapid nutrient recycling (Ripple & Beschta, 2005; Smith et al., 2003). The trees and other riparian vegetation stabilise streambanks, curb erosion, and restore river channels (Beschta & Ripple, 2012; Ripple & Beschta, 2004). Astute readers will have realised here that we have come full circle, from soil to top carnivores (bottom-up effects) and now from top carnivores back to soil (top-down effects). One can say, without exaggeration, that wolves help keep our whole life-support system balanced.

Man's Best Friend

Wolf effects, finally, cascade into net beneficial effects on specific human communities. True, wolves occasionally kill livestock. Yet cattle losses, for example, are due overwhelmingly to disease, weather, calving complications, theft, poison, and old age, and only a small per cent to predation. Moreover, one study found that 38% of such livestock

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loss was due to coyotes and feral dogs but only 1% to wolves (NRDC, 2009). By killing so many coyotes, then, wolves are no doubt good for ranchers on balance. Other studies found only tiny per cents of the biomass consumed by wolves to be livestock (Fuller 1989). Further, some of this biomass simply resulted from wolf scavenging on coyote kills (Fritts & Mech, 1981). When wolves do kill livestock, ranchers are compensated for their losses (NRDC, 2009). To the extent that ranchers thrive, large, open and undeveloped tracts of natural space are preserved, suggesting a natural, environmentalist-rancher alliance. With the relevant informational resources, then, students can help ranchers and the broader public understand the contributions of wolves, reduce wolf predation on livestock, and secure quick and generous compensation for losses.

Other human groups benefit. By preventing overshoots of ungulate populations and therefore the real possibility of disease, wolves are of benefit to hunters. Farmers and gardeners experience less crop damage (Ripple & Beschta, 2005). Drivers have fewer run-ins with large herbivores, and so law enforcement and taxpayers have lighter burdens. Homeowners experience fewer coyote-killed pets. They, as well as logging companies and others, benefit from healthier tree stands that contribute to commercial forest regeneration, reduce the possibility and severity of forest fires, and promote carbon sequestration, thereby lowering the negative impacts of global warming (Ripple & Beschta, 2005). Wolves also help local economies. Tourists coming to see wolves in Yellowstone bring in $35 million annually to the area (NRDC, 2009).

Student Exercises

Yet scientific knowledge is not enough. Students need personal engagement in the form of drama, participation in natural settings and the like to connect with the environment beyond mere abstraction and to act on that knowledge (Ballantyne, Anderson, & Packer, 2010; Bell. Russell, & Plotkin, 1998; Tsevreni, 2011). The following student exercises are offered to that end. While not classroom tested, they are similar to others I have used with success in environmental courses (Kowalewski, 2002). Some may be best suited for lower educational levels, some for higher, and others for all levels.

- Each student dresses up like a species or group of species, and all except the 'wolves' are positioned in their 'natural habitat' on a 'landscape' (e.g., gymnasium, schoolyard, or preferably large natural area). The 'wolves' then enter the scene and all students respond according to the scientifically researched direct and indirect effects. A video is made to show students afterwards.
- Students construct a table-top scene with cardboard cutouts of wolves and all the species they affect, then add or remove species as wolves are added or removed.
- Students are given vegetative, topographical, and road maps of an area, then show on the maps what changes occur when wolves are introduced.
- Each student is assigned a species affected by wolf introduction (e.g., coyote, elk, cardinal); they then sit in a circle telling how they feel when they hear wolves howling in the distance.
- Debate question: Should hunting of wolves be legal?
- Students write and collectively deliver a speech given by a wolf asked to speak to a gathering of ranchers upset at wolf predation on their cattle and sheep. Same question for gatherings of deer and elk hunters, logging companies, legislators, and wildlife managers.
- Generate a multivariate and multidisciplinary computer model, with stocks and flows, of the important causes and effects of wolf activity in a mixed forest, riparian, and meadow environment (for an example, see Kowalewski & Hoover, 1995).

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Broader Lessons for Environmental Educators

In short, as a large group of academic researchers recently stated boldly in the prestigious journal *Science*, 'top-down forcing must be included … [for] understanding nature' (Estes et al., 2011, p. 306). Anything less than that is a woefully incomplete picture.

Yet thinking about nature is one thing, thinking about our thinking is another. Trophic cascades argue for even broader lessons that can be highlighted for students as more effective ways to think about nature than the ones we have used in the past:

Indigenous wisdom

A wolf tracker once told me about an unfamiliar Ojibwe medicine man who unexpectedly came up and said: 'I had a dream about you. You are helping to save the wolves. When the wolves are safe, our people will be safe.' Is this 'magical thinking' or 'hard science'? The evidence suggests that here, and undoubtedly elsewhere as well, the mystical and the empirical coincide. The wolf and every other species, as natives insist, are good for you and me. Wolves, as we've seen, kick-start a cascade of effects that benefit a host of species, including our own. The lesson is clear — it may be necessary in many cases to decolonise the largely white, western field of environmental education, stop privileging modern expertise, and foreground indigenous ways of knowing (Root, 2010). In a supreme ironical twist, it is the most modern scientific findings that are telling us that.

Multidisciplinarity

Biology is not academic destiny, but in fact only part of a huge picture. Each species, like the wolf, affects and is affected by many arenas — economics, culture, and so on. Trophic cascades call for more polymath environmental educators, interdisciplinary courses, and team teaching. Privileging biology and the other physical sciences is not only ecologically unwarranted, but is perhaps the main reason the public remains so desultory about healing the earth. By teaching all aspects of the environment at the same time we can go far in making it more relevant and interesting to students and public alike. In the end, biology itself will be enriched.

Circular modelling

What goes around, they say, comes around. A wise proverb to be sure. Trophic cascades show us the futility, indeed the downright wrongheadedness, of linear models. Everything affects everything else, ultimately, in the single energy system we call nature. Everything we do, then, comes back to help us or haunt us, in the form of a gentle wave or a tsunami. Circular reasoning, heretofore disparaged, needs to be encouraged. 'May the circle be unbroken' is simply good pedagogy.

Ecosystem fragility

Ecosystems can change dramatically in a short time with just the gain or loss a single species. A single one can restructure a whole ecosystem. This is a truly cautionary tale. Losing just one species can cascade down to just about everywhere. On the other hand, if we respect biodiversity and can save a single endangered predator like the wolf, we can help save whole ecosystems. Predators in fact support our own life-support system. Each one is precious — pragmatically so.

Human hubris

A spiritual teacher once wrote, 'You cannot control nature, for nature controls you' (Ingerman, 1997, p. 143). The more we separate from nature, the more ecosystems become

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unsustainable. Trophic cascades teach us the illusion of human domination. Arguably, wolves affect us as much as we affect them. The notion that we are separate is overwhelmingly overturned by the scientific evidence — and the howlings of wolves.

Conclusion

Students, as research has shown, will shape the future debate about ecosystem health (Rickinson, 2001). Teaching them trophic cascades provides them with powerful intellectual resources to influence that discussion. They will understand why the Blackfeet have tales showing how wolves go out of their way to help humans (Grinnell, 2005). Ironically, they will show the public that the species most persecuted by humans on the planet is now responsible, by their contributions to saving that planet, for helping its persecutors become more healthy, wealthy, and wise.

Keywords: trophic cascades, gray wolves, endangered species, co-evolution, ecosystem dynamics

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