Title: Of wolves, elk and willows: how predation structures ecosystems

ABSTRACT PAGE

The Issue
Elimination of top predators (e.g. wolves) from regions like the Greater Yellowstone Ecosystem leads to changes in prey population density and behavior, as well as overall community structure. This issue addresses how ecosystems change when predators are removed, and what happens in such a system when the predators are restored. It is designed to address students' misconception that predators only influence ecosystems directly through predation. In the Greater Yellowstone Ecosystem, wolves exert impacts not only on their prey (elk) but also on lower trophic levels (e.g. willows).

Ecological Content
predation, trophic cascades, keystone species, direct vs. indirect effects, top-down vs. bottom-up effects, predator control, predation risk, prey behavior

Student-active Approaches
pairs share, hypothesis development, informal group work

Student Assessments
formulate hypotheses, essay quiz, minute paper, and concept map

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Citation
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Cover Image: *Cover photo elk.gif*

Image Caption: Elk browsing among cottonwood trees in the winter along the Lamar River in the Northern Range of Yellowstone National Park, during the period when wolves were not present. From Ripple and Beschta (2004b).

OVERVIEW PAGE

What Is the Ecological Issue?

Predator-prey interactions are among the most familiar and important in ecology, and they are also fraught with common misconceptions for students and the lay public. Many assume that the only important impact of such interactions is through direct population size control of prey by the predator (Stamp et al. 2006, Stamp and Armstrong 2007). The notion of potential indirect impacts of predator on prey has not occurred to most students, nor has the idea of *trophic cascades*, in which the impact of top predators on herbivores is also felt at the level of primary producers, where it impacts variables such as age structure, spatial distribution, or species composition (Pace et al. 1999, Ripple and Beschta 2004b, 2005, 2007; Ripple et al. 2001). This Issue uses the example of wolf extirpation and restoration in the Greater Yellowstone region to address the nature of trophic interactions, both direct and indirect.

Background

Wolves were extirpated in the Northern Range of Yellowstone by 1926 (Ripple and Beschta 2004a,b), and elk populations were fairly closely monitored in the Park beginning around the same time. On their winter range, elk may rely on woody vegetation as an important source of nutrition when grass and forbs become unavailable. Park managers became increasingly aware of changes in the woody riparian vegetation in valleys where the elk over-wintered, but despite human culling of the elk herd (from mid-1920's to 1968) the abundance of tall willows declined sharply, and there was little or no recruitment of cottonwood seedlings after the 1930's (Beschta 2003, 2005; Ripple and Beschta 2004 a,b). Park and range managers debated whether elk population densities were responsible for loss of native vegetation, or whether drought and climatic shifts were the culprit (Anderson and Blackford 2005; Yellowstone National Park 2007). Restoration of wolves in Yellowstone began in 1995, with significant and sometimes unexpected consequences for their elk prey and the woody browse used by elk in their winter range.

In this issue, students will study figures and generate hypotheses about why woody vegetation recruitment declined in Yellowstone National Park. Then, through a progressive disclosure approach, they will be shown data to help refute or support various hypotheses and finally construct a detailed food web concept map showing various trophic level interactions in the Yellowstone ecosystem, allowing them to see first hand how trophic cascades can structure ecosystems.

References

Note: Many of these references are available as PDFs in the Resource section.

- Anderson, R.J. and T. Blackford, eds. 2005. Ten years of Yellowstone wolves. *Yellowstone Science* **13**:1-48.
- Beschta, R.L. 2003. Cottonwoods, elk and wolves in the Lamar Valley of Yellowstone National Park. *Ecological Applications* **13**: 1295-1309.

- Beschta, R.L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowtone's Northern Range. *Ecology* **86**:391–403.
- Ripple, W.J. and R.L. Beschta. 2004a. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. *Forest Ecology and Management* **200**:161-181.
- Ripple, W.J. and R.L. Beschta. 2004b. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* **54**:755-766.
- Ripple, W.J. and R.L. Beschta 2005. Linking Wolves and Plants: Aldo Leopold on Trophic Cascades. *BioScience* **55**: 613-621.
- Ripple, W.J. and R.L. Beschta 2007. *Biological Conservation* **138**:514-519.
- Ripple, W. J., E.J. Larsen, R.A. Renkin, and D.W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* **102**:227-234.
- Pace, M.L., J.J. Cole, S.R. Carpenter and J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**:483-488.
- Stamp, N., M. Armstrong and J. Biger. 2006. Ecological misconceptions, survey III: The challenge of identifying sophisticated understanding. *Bulletin of the Ecological Society of America* **87**:168-175. http://www.esajournals.org/perlserv/?request=get-toc&issn=0012-9623&volume=87&issue=2
- Stamp, N. and M. Armstrong. 2007. Overcoming ecological misconceptions: Using the power of story. http://ecomisconceptions.binghamton.edu/index.htm site visited January 2008.
- Yellowstone National Park. 2007. Yellowstone Elk**.** http://www.nps.gov/yell/naturescience/elk.htm site visited January 2008.

FIGURE SETS PAGE

Figure Set and Ecological Question	**Student-active Approach**	**Cognitive Skill**	**Class Size/Time**
Fig. Set 1: Changes in cottonwood and willow abundance in the 20th century. (Beschta 2003; Ripple & Beschta 2004a)	Pairs share and hypothesis development	Knowledge, comprehension, interpretation, analysis	any/moderate
Fig. Set 2: Factors influencing suppression and recrutiment of woody riparian vegetation. (Beschta 2003; Ripple & Beschta 2004a)	Pairs share and report out	Knowledge, comprehension, interpretation, analysis	any/moderate
Fig. Set 3: Causes of intense elk browsing on cottonwoods and willows during the 20th century. (Ripple & Beschta 2004a)	Pairs share	Knowledge, comprehension, interpretation	any/short
Fig. Set 4: How **do** wolves impact elk and elk browsing, if not by direct population control? (Ripple & Beschta 2004b)	Informal group work	Knowledge, comprehension, interpretation, application, synthesis	any/moderate to long

RESOURCES PAGE

Beschta and Ripple Scientific Papers

*PDFs of all of the main articles cited in this Issue, including those from which figures were used (marked by *). Links to these and more related articles at: http://www.cof.orst.edu/cascades/articles.php*

*Ripple, W.J. and Beschta, R.L. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138, June 2007: 514-519.

Beschta, Robert L., and Ripple, William J. 2007. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. Western North American Naturalist 67(4), 2007: 613-617.

Ripple, W.J. and Beschta, R.L. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230, 2006: 96-106.

Beschta, R.L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's Northern Range. Ecology 86(2), 2005: 391-403.

Ripple, W.J. and Beschta, R.L. 2005. Willow thickets protect young aspen from elk browsing after wolf reintroduction. Western North American Naturalist 65(1), 2005: 118-122.

*Ripple, W.J. and Beschta, R.L. 2004a. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. Forest Ecology and Management 200, 2004: 161-181.

*Ripple, William J. and Beschta, Robert L 2004b. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience Vo.l 54 No. 8, August 2004: 755-766.

*Beschta, R.L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications 13(5), 2003: 1295-1309.

Concept Mapping

Explanations and examples of how to build concept maps and their utility for teaching:
How to construct a concept map
(http://www.udel.edu/chem/white/teaching/ConceptMap.html)

Concept mapping
(http://www.cotf.edu/ete/pbl2.html)

The Concept mapping homepage
(http://users.edte.utwente.nl/lanzing/cm_home.htm)

Cottonwoods
Good photos of cottonwoods as well as general background information.
Narrowleaf cottonwood. USDA & NRCS Plant Guide.
(http://plants.usda.gov/plantguide/doc/cs_poan3.doc)

Elk
Applied Animal Behavior Project of the University of Idaho and Washington State University. – *general information on elk behavior*
(http://www.cnr.uidaho.edu/range556/Appl_BEHAVE/)

Wild Nature Images. *Great photos of elk and other wildlife.*
(http://www.wildnatureimages.com/elk%202%20Y.htm)

Yellowstone Elk. Yellowstone National Park. *Information on the history of elk populations in the Park, as well as their interactions with human visitors.*
(http://www.nps.gov/yell/naturescience/elk.htm)

Related Newspaper and Magazine Articles
Environmental Magazine – *Good article to show the human side of science, and how Ripple and Beschta stumbled onto the trophic cascade issue in Yellowstone*
(http://findarticles.com/p/articles/mi_m1594/is_2_17?pnum=3&opg=n16129805)

National Wildlife Federation – *Good general article about Ripple, Beschta and other scientists working on the trophic cascade question in Yellowstone*
(http://www.nwf.org/nationalwildlife/article.cfm?articleId=829&issueId=69)

Mystery in Yellowstone: wolves, wapiti, and the case of the disappearing aspen. Notable Notes, Oregon State University 2004.

New York Times – *Good general article about the trophic cascade question and wolves in Yellowstone*
(http://www.nytimes.com/2005/10/18/science/earth/18wolf.html)

High Country News – *Short article about scientific debate surrounding wolf trophic cascade in Yellowstone, and alternative explanations for increase in willow cover* (http://www.hcn.org/servlets/hcn.Article?article_id=17471)

Trophic Cascades

History of the concept, background information, and links to many related articles.
Oregon State University College of Forestry – Trophic Cascades Program
(http://www.cof.orst.edu/leopold/)

Ripple, W.J. and Beschta, R.L. Linking Wolves and Plants: Aldo Leopold on trophic cascades. BioScience Vol. 55 No. 7, July 2005: 613-621.

Wolves

UC Berkeley News story about benefit to scavengers of wolf kills in Greater Yellowstone Ecosystem.
(http://www.berkeley.edu/news/media/releases/2003/11/04_wolves.shtml)

Wild Nature Images. *Great photos of wolves and other wildlife.*
(http://www.wildnatureimages.com/Wolf_and_Bear.htm)

Information on the history of wolf restoration in Yellowstone National Park, including details of their interactions with and impact upon elk and other ungulates, other predators, livestock, human visitors and ranchers:
Wolves of Yellowstone. Yellowstone National Park.
(http://www.nps.gov/yell/naturescience/wolves.htm)

Ten Years of Yellowstone Wolves. Yellowstone Science.
(http://www.nps.gov/yell/planyourvisit/upload/YS13(1).pdf)

Yellowstone National Park

General information on and photos of Yellowstone National Park and its history.
Yellowstone National Park. Wikipedia.
(http://en.wikipedia.org/wiki/Yellowstone_National_Park)

Yellowstone National Park. National Park Service official site.
(http://www.nps.gov/yell/index.htm)