# Carrion – It's What's for Dinner: WOLVES REDUCE THE IMPACT OF CLIMATE CHANGE

JUANITA M. CONSTIBLE LUKE H. SANDRO RICHARD E. LEE, JR.

# The Big Bad Wolf

Humans have viewed wolves as competitors, threats to personal safety, and symbols of evil throughout history. By the early part of the 20th century, gray wolves (*Canis lupus*) had been eradicated from 42% of their historic range in North

Table 1. Brief history of gray wolves in Yellowstone National Park.			
1872	Yellowstone National Park (YNP) is established by an act of the U.S. Congress.		
1872-1917	Wolves in and around YNP are killed for pelts, to protect humans and livestock, and for sport.		
1918	The newly-formed National Park Service takes control of YNP and continues to hunt wolves.		
1926	Wolves are extirpated from YNP.		
1973	The U.S. Government lists the gray wolf as an endangered species.		
1995-1996	Thirty-one wolves are reintroduced into YNP.		

Source: Phillips and Smith, 1996

America (Laliberte & Ripple, 2004). In Yellowstone National Park, gray wolves were hunted to local extinction by 1926, but were reintroduced in 1995 after a decades-long process involving biologists, politicians, ranchers, and the general public (Table 1). By the end of 2006, the wolf population in the park was at least 136 wolves in 13 packs (Smith et al., 2007).

In this activity, high school students use mathematical models to explore how the presence of wolves buffers other carnivores and scavengers from the effects of climate change. By the end of the lesson, students should be able to:

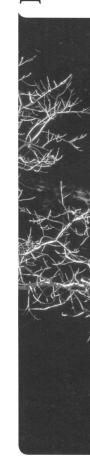
- define and give examples of keystone species.
- demonstrate, using mathematical models, that ecosystems are more resilient to environmental change when they contain a full complement of species, including top carnivores.
- recognize that math is a vital tool in scientific investigations.

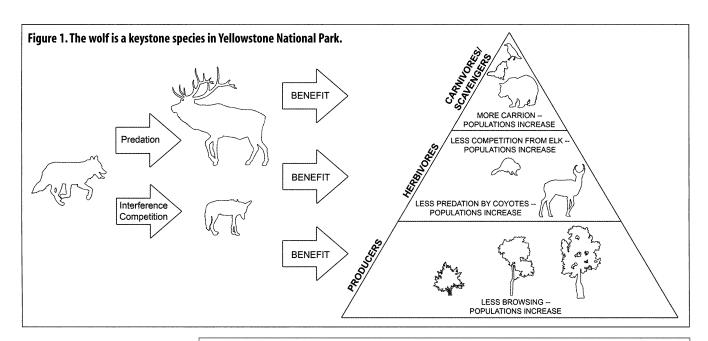
JUANITA M. CONSTIBLE is Laboratory Coordinator and Science Writer, Department of Zoology, Miami University, Oxford, OH 45056; e-mail: bufohemiophrys@hotmail.com. LUKE H. SANDRO is a high school biology teacher at Springboro High School, Springboro, OH 45066; e-mail: lsandro@springboro.org. RICHARD E. LEE, JR. is Distinguished Professor of Zoology, Department of Zoology, Miami University, Oxford, OH 45056; e-mail: leere@muohio.edu.

# Background

From an ecological perspective, it was important to restore the gray wolf to Yellowstone because it is a keystone species. Keystone species, which are usually top predators, affect their communities or ecosystems in a much larger way than expected based on abundance alone (Steneck, 2005). The presence, abundance, and productivity of a wide array of species in Yellowstone National Park are indirectly affected by interactions of wolves with elk and coyotes (Figure 1).

For example, the reintroduction of wolves has facilitated the recovery of beavers in Yellowstone. In the 1800s, human trappers decimated beaver populations. After wolves were removed from the park, elk populations grew and competition for willow - the preferred food and construction material of beavers - became intense (Ripple & Beschta, 2003). Although beavers had been protected from trapping since the early 1920s, and beaver reintroduction efforts were underway, competitive pressure from elk suppressed recovery (Baker et al., 2005). Since wolves were restored to Yellowstone, predation, hunting, and drought have reduced elk populations. But elk also have changed their behavior (Creel et al., 2005): When elk detect wolves in a general area, they move toward conifer forests (where they have good protection from wolves) and away from open areas and streams (where they have less protection from wolves; Figure 2). Because of the combined effect of fewer elk and reduced use of willow habitat, the number of beaver colonies (five to six beavers per





colony) on the northern range of Yellowstone increased from one in 1996 to nine in 2003 (D.W. Smith, 2006, personal communication).

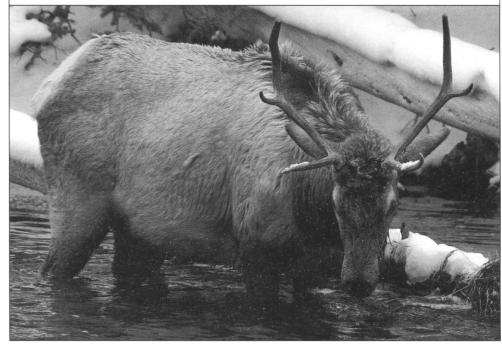
# Winter on the Northern Range

In Yellowstone National Park, daytime winter temperatures range from -40° C to -5° C and snow depths can exceed 7m at high elevations (NPS, 2006). Every autumn, the northern Yellowstone elk herd migrates from high-elevation summer habitat within the park to milder habitat in the northern range, a 1,530 km<sup>2</sup>-area that includes a portion of the park and some adjacent public and private land (Singer & Mack, 1999). Even so, winter isn't easy. Elk search for grasses and other herbaceous plants by digging

in the snow with their hooves. When the snow is deep or covered by a hard crust, digging becomes more difficult, as does the simple act of moving through the snow (Gese et al., 1996). Furthermore, the plants under the snow are less nutritious than in the summer (Jenkins & Starkey, 2003). In severe winters, elk regularly starve to death (Wisdom & Cook, 2000). They also can suffer the same fate during mild winters if conditions during the previous summer were poor (Vucetich et al., 2005).

Carcasses – particularly those of elk – are an important food source for Yellowstone's carnivores. Many carnivores such as bears and eagles scavenge carrion during the winter and early spring (Figures 1 and 3). Some species, such as ravens, have even learned to track wolves to kill sites (Stahler et al., 2002). Before wolves were restored to Yellowstone, carrion

Figure 2. An elk forages in a stream during winter. Photograph courtesy Ed Thomas.



availability depended on winter severity. In winters with deep snow and low temperatures, elk carrion was plentiful; in mild winters, carrion was sparse. During the rest of the year, carrion was negligible (Gese et al., 1996). Even in the presence of wolves, snow cover plays a role in the amount of carrion in the park. Wolves leave more carrion for scavengers when snow is deep because elk are easier to kill and wolf packs eat a smaller proportion of each kill. However, the presence of wolves also has altered the timing of carrion in the park; carrion is now available year-round, regardless of the snow cover, and is a more predictable resource for scavengers (Wilmers et al., 2003a). The change in the timing and predictability of carrion benefits both small scavengers (e.g., foxes), which have small stores of body fat and need to feed frequently, and large scavengers (e.g., bears), which require a high-energy food source before hibernation (Wilmers & Getz, 2005).

No other carnivores in Yellowstone fill the ecological role of the gray wolf. Coyotes occasionally kill elk, but primarily feed on small mammals and carrion (Crabtree & Sheldon, 1999). Bears also will prey on elk, but only during some parts of the year. Cougars are a major year-round predator of elk, but defend their kills from scavengers more fiercely than wolves and hide uneaten prey (Berger & Smith, 2005). Finally, human hunters provide large amounts of carrion in the form of gut piles on the park borders, but only from early January to mid-February. Bears in hibernation cannot take advantage of mid-winter gut piles, and scavenging coyotes have difficulty finding the gut piles and are often shot by human hunters (Wilmers et al., 2003b).

#### Let it Snow!

As global temperatures rise, winter precipitation will fall as rain more often than as snow, and snowmelt will occur earlier in the spring (Barnett et al., 2005). Since 1948, winter temperatures have increased, the monthly

snow depth has decreased, and the snow season has gotten shorter in the northern part of Yellowstone. Using mathematical models, two scientists in California demonstrated that although less carrion is available to scavengers as snow cover declines, the reduction is less dramatic when wolves are present in the park (Wilmers & Getz, 2005). In essence, wolves act as a "buffer" against climate change by providing more carrion: They delay the detrimental effects of declining snow cover such that other species have more time to adapt to their changing environment. The presence of wolves might be especially important to threatened species such as grizzly bears. Climate change and disease have reduced the availability of whitebark pine (Pinus albicaulis), one of the few high-quality food sources available to Yellowstone bears in autumn. Wolfkilled elk may give bears time to adapt to a new food source (Smith & Ferguson, 2005).

# Starting the Activity

Before class starts, write this question on the board: Why are carnivores important in ecosystems?

Figure 3. After wolves killed this bison and had eaten their fill, the carcass was picked clean by scavengers. Note how the snow around the carcasses has been churned up by a large number of animals. Photograph courtesy Ed Thomas.



Table 2. Internet resources for introducing Carrion – It's What's for Dinner.

- Red fox feeding on a moose carcass: <a href="www.admin.mtu.edu/urel/breaking/2006/Videos/redfox.mov">www.admin.mtu.edu/urel/breaking/2006/Videos/redfox.mov</a>
- Wolves feeding on an elk carcass: www.nps.gov/archive/yell/tours/thismonth/nov2004/wolves/index.htm
- Electronic Field Trip of Yellowstone National Park: www.windowsintowonderland.org/orientation/pages/index.html
- Video of park ranger discussing wolves: <a href="https://www.windowsintowonderland.org/wolves2/teacherinfo.shtml">www.windowsintowonderland.org/wolves2/teacherinfo.shtml</a>
- Yellowstone Park Digital Slide File: www.nps.gov/archive/yell/slidefile/index.htm

As students enter the room, engage their attention by playing a soundtrack of wolves howling and/or a video or slide show of Yellowstone carnivores/scavengers hunting or eating prey (see Table 2 for resources). Once students are seated, draw attention to the question on the board, and explain that today's class will focus on gray wolves in Yellowstone National Park. Introduce the term *keystone species*. Introduce the park with a short slide show or video (see Table 2 for suggested resources). Include the history of wolves in the park (Table 1).

### **Student Worksheet**

This activity may be done individually, in small groups (two to four students), or as a class. You will need 1.5 to 2.5 hours to complete this activity. Have students read each of the following sections (starting with "Meet Dr. Chris Wilmers!") and answer the associated questions. You may wish to circulate around the class to ensure that students are answering the questions thoughtfully.

#### Meet Dr. Chris Wilmers!

Today you will learn about cutting-edge research by an ecologist named Dr. Chris Wilmers (Figure A). Wilmers started studying wolves when he was a graduate student at the University of California-Davis. He was interested in interactions between wolves and their prey, and quickly realized that climate had a big impact on those interactions. In collaboration with his advisors, Drs. Wayne Getz and Eric Post, Wilmers investigated how climate change might influence the relationship between different feeding levels in the Yellowstone food web. Dr. Wilmers began working as a professor at the University of California-Santa Cruz in January 2007, where he plans to continue his Yellowstone research.

Figure A. Dr. Wilmers uses radio telemetry to locate wolves in Yellowstone National Park. Photograph courtesy Chris Wilmers.



#### The Predictions

Recall that your teacher told you wolves were eliminated from Yellowstone National Park in 1926, but were restored to the park 70 years later. When Wilmers and Getz were studying the impacts of climate change on the Yellowstone food web, they made two general predictions:

Prediction 1: As global temperatures rise, northern and high altitude areas will experience warmer and shorter winters.

Prediction 2: Climate change will be less harmful to ecosystems with top predators than to ecosystems without them.

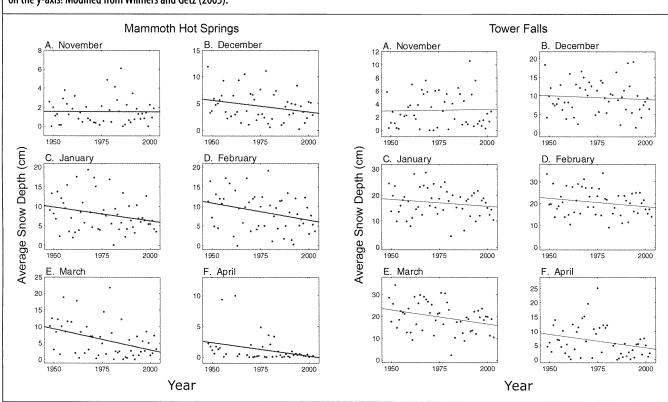
#### **Snow Depth Data**

The scientists obtained climate data from two weather stations in Yellowstone: Mammoth Hot Springs, which is near the northern entrance to the park, and Tower Falls, which is about 39 km east of Mammoth. First, the scientists graphed the average monthly snow depth for each year from 1950-2000. Then they used a statistical technique called *regression* to draw a line – called a *line of best fit* – that approximated the best overall relationship between the points. In Figure B, you will see the lines of best fit for each month. Remember that the lines indicate general trends – that is, whether the average snow depth for that month has shown an overall increase, decrease, or no change during the 50-year period.

Answer these questions:

- 1. How has snow depth changed overall from 1950 to 2000?
- 2. Is the trend the same or different for each weather station? Explain how.
- 3. Is the trend the same or different in each month? Explain how

Figure B. Change in snow depth from 1950-2000 at two weather stations in Yellowstone National Park. Note: Each graph shows a different scale on the y-axis! Modified from Wilmers and Getz (2005).



- 4. a. Is the effect of warming stronger at the beginning or the end of winter?
  - b. Why might this be?
- 5. a. Does Figure B support Prediction 1?
  - b. Why or why not?
  - c. What other data would be useful? Be specific.

#### **Snow Cover Data**

Wilmers and Getz also recorded the last day of snow cover at Mammoth Hot Springs and Tower Falls (see Figure C). For each year, they plotted the number of days it took after January 1 for the snow to melt enough to reveal bare ground. Once again, the scientists used lines of best fit to estimate the trend in snow cover for each station.

Answer this question:

6. How has the length of the snow season changed overall from 1950 to 2000?

#### Maximum Temperature Data

Finally, the researchers graphed the number of days from January through March that temperatures were above freezing (see Figure D). TMAX is the maximum temperature in a given day.

Answer these questions:

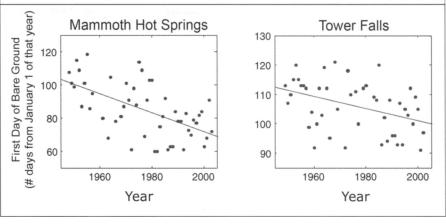
- 7. How has the number of warm days changed from 1950 to 2000?
- 8. a. When considered together, do Figures B, C, and D support Prediction 1?
  - b. Why or why not?
  - c. What other data would be useful? Be specific.

# Availability of Carrion

Winter is a tough time for large herbivores like elk. Food is in short supply and is hard to find, and it takes a lot of energy for elk just to move around in deep snow. The result is that many elk starve to death. In elk populations with no predators, deep snow is one of the main reasons elk die in the winter. However, what's bad for elk is good for ravens, eagles, coyotes, and bears. *Carrion* (rotting flesh) is a vital food source for these scavengers.

The researchers used a simple equation to estimate the amount of carrion that was available to scavengers when an elk died, before wolves were reintroduced to the park in 1995. The equation describes a line of best fit constructed in the same general way as for the climate data, above. In this case, the researchers started with a scatter plot showing snow depth on the x-axis and the amount of carrion on the y-axis. The

**Figure C. Change in length of snow season from 1950-2000 at two weather stations in Yellowstone National Park.** Note: Each graph shows a different scale on the y-axis! Modified from Wilmers and Getz (2005).



**Figure D. Change in number of warm days from 1950-2000 at two weather stations in Yellowstone National Park.** Note: Each graph shows a different scale on the y-axis! Modified from Wilmers and Getz (2005).

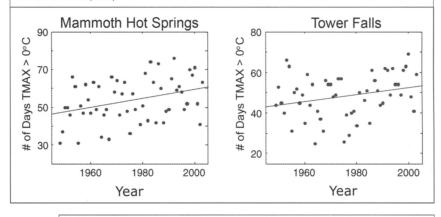
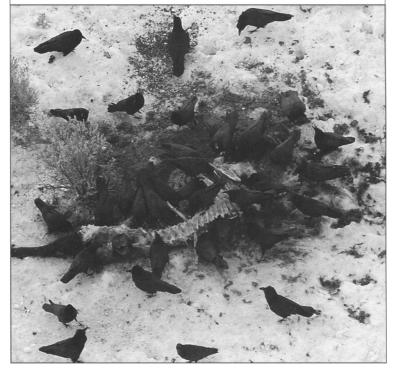


Figure E. Ravens feeding on carrion. Photograph courtesy Yellowstone Wolf Project.



data used to construct Equation 1 were drawn from a study on coyotes done before wolves were reintroduced to the park.

(Does Equation 1 look familiar? It should, because you've used it in math class before. It's y = mx + b!)

Fill in the values for  $C_{without\ wolves}$  in Table A, and then answer this question:

Explain the relationship between snow depth and the availability of carrion when there are no wolves present.

Before wolves were reintroduced to Yellowstone, the main cause of elk deaths during the winter was starvation due to deep snow. Once wolves were reintroduced to the park, however, predation became the main cause of death in elk. Since reintroduction, the availability of carrion for scavengers has depended on three things: snow depth, wolf pack size, and how much of a carcass each wolf pack eats.

Look at Table B, which shows how snow depth affects the eating behavior of wolves.

Answer these questions:

- 10. a. How do wolves change their eating behavior when there is less snow?
  - b. Why do you think this might occur? (Note: Think about how snow depth might affect the hunting ability of wolves. Remember that wolves weigh a lot less than elk do.)

Once we have used S to get E, we can complete Equation 2. (The number 0.68 refers to the edible proportion of each elk carcass.)

Equation 2: Amount of carrion with wolves = Pack size  $x = \begin{bmatrix} 30 \end{bmatrix} x$   $Kill rate \Rightarrow x$  (1-Proportion Eaten)  $x = \begin{bmatrix} 0.68 \end{bmatrix}$  Also expressed as:  $C_{with wolves} \Rightarrow E_{with wolves} \Rightarrow E$ 

In the late winter, each wolf in Yellowstone kills an average of 240 kg/wolf/month (just over 2 elk per month). There are over 30,000 elk spending the summers in the park, and over 47,000

THE AMERICAN BIOLOGY TEACHER, VOLUME 70, NO. 2, FEBRUARY 2008

elk spending the winters in the park and the nearby northern range.

Fill in the values for  $C_{with wolves}$  in Table C, and then answer these questions:

- Explain the relationship between snow depth and the availability of carrion when there are wolves present.
- 12. Compare and contrast the availability of carrion at different snow depths, with and without wolves.

# Modeling the Effects of Climate Change on Carrion

Wilmers and Getz used the equations you just worked with to create a mathematical model of the change in carrion availability between 1950 and 2000. A mathematical model is a tool for examining how a system or process would behave differently under different conditions. In this case, the "system or process" is the availability of carrion to scavengers, and the "different conditions" are climate change and the presence or absence of wolves.

The scientists included two scenarios in their model. In Scenario 1, they assumed there were no wolves in the park (which in fact was true until 1995). They selected 100 random snow depth values for each

able to scavengers per week with no wolves present in Yellowstone National Park.				
S	C <sub>without wolves</sub>			
(Snow depth)	(Amount of carrion)			
15 cm	ka			

kg

kg

10 cm

5 cm

Table A. Estimate of the amount of carrion avail-

Table B. Proportion of elk carcass eaten by a typical wolf pack in Yellowstone National Park.

S	E	
(Snow depth)	(Proportion eaten)	
15 cm	0.29	
10 cm	0.31	
5 cm	0.32	

Table C. Estimate of the amount of carrion available to scavengers per month with wolves present in Yellowstone National Park. At the time of the Wilmer and Getz study, the average pack size was 11 wolves. In 2006, packs ranged from 4-19 animals (average = 10).

S (Snow depth)	P (Pack size)	K (Kill rate)	E (Proportion eaten)	C <sub>with wolves</sub> (Amount of carrion)
15 cm	11	8 kg/wolf/day	0.29	kg
10 cm	11	8 kg/wolf/day	0.31	kg
5 cm	11	8 kg/wolf/day	0.32	kg

month in the winter of 1950. Then they selected 100 random snow depth values for each month in the winter of 2000. The scientists used each of these values in Equation 1. In other words, instead of calculating  $C_{\rm without\ wolves}$  three times, like you did in Table A, they calculated  $C_{\rm without\ wolves}$  1200 times! For each run of the scenario, Wilmers and Getz calculated the difference between the amount of carrion in 1950 and the amount of carrion in 2000. Finally, they graphed those average monthly differ-

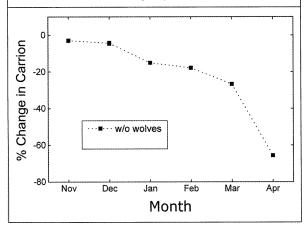
ences (see Figure F).

Answer this question:

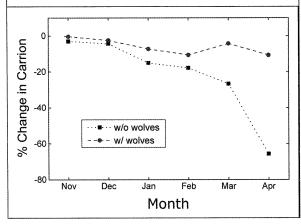
13. How has the availability of carrion changed between 1950 and 2000?

In Scenario 2, Wilmers and Getz asked, "What if?" and pretended that wolves had been present in the park for the entire 50 years. They used the same snow

**Figure F. Estimated monthly change in carrion between 1950 and 2000, in the absence of wolves.** Note: The model was run only for 1950 and 2000, not any of the years in between. Each point on the line represents the difference between the two years. Modified from Wilmer and Getz (2005).



**Figure G. Estimated monthly change in carrion from 1950 to 2000, with and without wolves.** Note: The model was run only for 1950 and 2000, not any of the years in between. Each point on the line represents the difference between the two years. Modified from Wilmers and Getz (2005).



depth values as in Scenario 1, but also chose random wolf pack sizes from 1 to 27. Once again, they calculated  $C_{\text{with}}$  wolves 1,200 times using Equation 2, calculated the differences between 1950 and 2000, and graphed the average monthly differences (see Figure G).

Answer these questions:

- 14. If wolves had not been eradicated from Yellowstone, how would the availability of carrion have changed between 1950 and 2000?
- 15. a. Does this model support Prediction 2?
  - b. Why or why not?
  - c. What other data would be useful? Be specific.
- 16. If wolves had not been reintroduced to Yellowstone, how do you think climate change (and resulting shorter winters) would affect eagles, bears, and other scavengers (who depend on carrion) in the future?

#### **Assessment & Extensions**

The correct answers for the student worksheets are:

Table A - 301 kg, 196 kg, 91 kg

Table C - 1275 kg, 1239 kg, 1221 kg

To encourage critical thinking about what the numbers actually mean, however, we suggest providing a rubric to students at the start of the activity that includes performance criteria on data interpretation and logical scientific explanations (Figure 4).

You may wish to extend this lesson by having your students consider another ecosystem in which top carnivores can ameliorate the effects of climate change. Since 1979, there have been dozens of massive bleaching events, in which reef-forming corals lost their symbiotic algae in response to high temperatures. Recovery, while possible, is impeded by other environmental threats such as predation by the crown-of-thorns starfish. Populations of starfish are kept in check partly by three commercially-prized predators, including the triton snail. Make some predictions about how climate change would affect coral reefs in the presence and absence of starfish predators. You can get more information from these Web sites:

- AIMS Research—Coral Bleaching: <a href="www.aims.gov.au/pages/research/coral-bleaching/coral-bleaching.html">www.aims.gov.au/pages/research/coral-bleaching/coral-bleaching.html</a>
- CoRIS—Hazards to Coral Reefs: <a href="www.coris.noaa.gov/about/">www.coris.noaa.gov/about/</a> hazards
- CRC Reef Research Center: <a href="www.reef.crc.org.au/discover/">www.reef.crc.org.au/discover/</a> plantsanimals/cots/cotstheory.html
- PBS Coral Reef Connections: <a href="www.pbs.org/wgbh/evolution/survival/coral/predators.html">www.pbs.org/wgbh/evolution/survival/coral/predators.html</a>

Alternatively, have your students explore the social and political ramifications of wolf reintroduction by imagining what each of the following stakeholders might have to say about wolf reintroduction:

- · A rancher, who raises sheep on the border of the park
- An environmentalist, who wants to preserve the natural environment of the park
- A tourist, who has come to the park to escape city life and to see wildlife
- A scientist, who studies interactions between predators and their prey
- A hunter, who has spent a large sum of money for a guided elk hunt north of the park

#### Conclusion

This activity is a good fit for multiple aspects of the high school life science curriculum and could be easily modified for use in a college-level ecology or environmental science course. The lesson addresses science education standards on populations, ecosystems, and environmental change (NRC, 1996) and students learn that math is a useful tool for answering complicated questions about the natural world. Finally, climate change lessons are often, by nature, full of doom and gloom. This activity suggests to learners that by protecting the integrity of ecosystems, humans can mitigate the effects of a warming world.

# Acknowledgments

This work was supported by National Science Foundation Grants OPP-0337656 and IBN-0416720. Thanks to Chris Wilmers and Doug Smith for sharing their expertise on wolves and for providing photographs. Ed Thomas provided additional photographs. We thank Heather Marshall and Luke Sandro's students (Springboro

Figure 4. Assessment rubric. Adapted from Lantz (2004).  Date:  Student Name(s):		Courties Viellowstone Wolf Project	
		ASSESSMENT	Photo courte
PERFORMANCE CRITERIA	POINTS POSSIBLE	SELF	TEACHER
My mathematical calculations are accurate.	5		
I described all trends, patterns, and relationships described by each graph and table.	10		
I made appropriate inferences and/or conclusions based on prior knowledge, background information, and the available data.	15		
I expressed my ideas clearly and logically.	15		
My spelling and grammar are correct.	5		
TOTAL	50		
NOTES:			

High School, Ohio) for piloting this activity. Evelyn Dietz, Nate Guerin, and two anonymous reviewers made valuable comments on an earlier draft of this manuscript.

### References

- Baker, B.W., Ducharme, H.C., Mitchell, D.C.S., Stanley, T.R. & Peinetti, H.R. (2005). Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological Applications*, 15, 110-118.
- Barnett, T.P., Adam, J.C. & Lettenmaier, D.P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, 438, 303-309.
- Berger, J. & Smith, D.W. (2005). Restoring functionality in Yellowstone with recovering carnivores: Gains and uncertainties. In J.C. Ray, K.H. Redford, R.S. Steneck & J. Berger (Editors), Large Carnivores and the Conservation of Biodiversity (pp. 100-109). Washington, DC: Island Press.
- Crabtree, R.L. & Sheldon, J.W. (1999). The ecological role of coyotes on Yellowstone's northern range. *Yellowstone Science*, 7, 15-23.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86, 3387-3397
- Gese, E.M., Ruff, R.L. & Crabtree, R.L. (1996). Foraging ecology of coyotes (*Canis latrans*): The influence of extrinsic factors and a dominance hierarchy. *Canadian Journal of Zoology*, 74, 769-783.
- Jenkins, K.J. & Starkey, E.E. (2003). Winter forages and diets of elk in oldgrowth and regenerating coniferous forests in western Washington. American Midland Naturalist, 130, 299-313.
- Laliberte, A.S. & Ripple, W.J. (2004). Range contractions of North American carnivores and ungulates. *BioScience*, 54, 123-138.
- Lantz, H.B. (2004). Rubrics for Assessing Student Achievement in Science Grades K-12. Thousand Oaks, CA: Corwin Press.
- National Park Service (NPS). (2006). Winter weather in Yellowstone. Available online at: <a href="http://www.nps.gov/yell/planyourvisit/weather.">http://www.nps.gov/yell/planyourvisit/weather.</a> httm.
- National Research Council (NRC). (1996). National Science Education Standards. Washington, DC: National Academy Press.
- Phillips, M.K. & Smith, D.W. (1996). The Wolves of Yellowstone. Stillwater, MN: Voyageur Press.

- Ripple, W.J. & Beschta, R.L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management, 184, 299-313.
- Singer, F.J. & Mack, J.A. (1999). Predicting the effects of wildfire and carnivore predation on ungulates. In T.W. Clark, A.P. Curlee, S.C. Minta & P.M. Kareiva (Editors), *Carnivores in Ecosystems: The Yellowstone Experience* (pp. 189-237). New Haven, CT: Yale University Press.
- Smith, D.W. (2006). Personal communication.
- Smith, D.W. & Ferguson, G. (2005). Decade of the Wolf: Returning the Wild to Yellowstone. Guilford, CT: The Lyons Press.
- Smith, D.W., Stahler D.R., Guernsey, D.S., Metz, M., Nelson, A., Albers, E. & McIntyre, R. (2007). Yellowstone Wolf Project: Annual Report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-01.
- Stahler, D., Heinrich, B. & Smith, D. (2002). Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour*, 64, 283-290.
- Steneck, R.S. (2005). An ecological context for the role of large carnivores in conserving biodiversity. In J.C. Ray, K.H. Redford, R.S. Steneck, and J. Berger (Editors), *Large Carnivores and the Conservation of Biodiversity* (pp. 9-33). Washington, DC: Island Press.
- Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005). Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos, 111, 259-270.
- Wilmers, C.C. & Getz, W.M. (2005). Gray wolves as climate change buffers in Yellowstone. *PLoS Biology*, 3, 0571-0576.
- Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M. (2003a). Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, 72, 909-916.
- Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W. & Getz, W.M. (2003b). Resource dispersion and consumer dominance: Scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters*, 6, 996-1003.
- Wisdom, M.J. & Cook, J.G. (2000). North American elk. In S. Demarais & P. R. Krausman (Editors), Ecology and Management of Large Mammals in North America (pp. 694-735). Upper Saddle River, NJ: Prentice Hall.