Some Animals Are More Equal than Others: Trophic Cascades and Keystone

OVERVIEW

The short film *Some Animals Are More Equal than Others: Trophic Cascades and Keystone Species* opens by asking two fundamental questions in ecology: "What determines how many species live in a given place? Or how large can each population grow?" The film then describes the pioneering experiments by Robert Paine and James Estes, in the 1960s and 1970s, which started to address them. Paine's experiments on the coast of Washington state showed that the starfish is a keystone species, having a disproportionately large impact on its ecosystem relative to its abundance. Estes and colleague John Palmisano discovered that the kelp forests of the North Pacific are indirectly regulated by sea otters, which feed on sea urchins that consume kelp. The presence or absence of sea otters causes a cascade of direct and indirect effects down the food chain, which in turn affect the structure of the ecosystem. These early experiments inspired countless others on keystone species and trophic cascades in ecosystems throughout the world.

KEY CONCEPTS

A. Keystone species have direct and indirect effects on the abundance and number of species in an ecosystem that are disproportionately large relative to their own abundance in the ecosystem.
B. Not all species in an ecosystem have strong interactions. The removal of some species has little or no effect on others.
C. Many keystone species are apex predators: predators at the top of a food web that are not preyed on by others.
D. Removal or addition of an apex predator that is a keystone species causes changes in the type and number of species, and their population sizes, at multiple trophic levels.
E. Keystone species are critical to maintaining the diversity and stability of an ecosystem.
F. Identifying the interactions among species in an ecosystem and determining how species numbers and population sizes are regulated requires experiments conducted over long time periods.

CURRICULUM CONNECTIONS

Standards	Curriculum Connections
NGSS (2013)	HS-LS2-1, HS-LS2-3, HS-LS2-6, HS-LS4-5; SEP6
AP Bio (2015)	4.A.5, 4.A.6, 4.B.3, 4.C.4; SP6
IB Bio (2016)	4.1, 4.2, C.1, C.2, C.3, C.4, C.5
AP Env Sci (2013)	II.A, II.B
IB Env Systems and Societies (2017)	2.2, 2.3, 2.4, 3.3
Common Core (2010)	ELA.RST.9–12.2, WHST.9–12.9
Vision and Change (2009)	CC4, CC5; DP1

PRIOR KNOWLEDGE

Students should:

- be familiar with the definitions of biological communities and ecosystems: a biological community is a group of interacting organisms, whereas the ecosystem also includes their environment (i.e., abiotic factors);
- be familiar with the concepts of food chains, food webs, and trophic levels and how energy flows from producers to primary consumers and then to the higher trophic levels of secondary and tertiary consumers/predators (carnivores and omnivores); and
- understand that a hypothesis is a potential explanation for an observation in nature.

PAUSE POINTS

The film may be viewed in its entirety or paused at specific points to review content with students. The table below lists suggested pause points, indicating the beginning and ending times in minutes in the film.

	Begin	End	Content Description	Review Questions
1	0:00	1:13	• Diverse habitats around the world are made up of communities of plants and animals. • Communities are made up of a variety of species. • Ecologists are interested in understanding what controls the number and types of species in an ecosystem.	• Why would it be important to understand what controls the number and types of species in an ecosystem?
2	1:14	4:05	• Prior to the early 1960s, most ecologists thought that the number of producers limits the number of herbivores, which in turn limits the number of predators. This “bottom up” explanation suggests that every trophic level is regulated by the level below it. • The bottom-up explanation did not explain why herbivore populations do not grow large enough to eat all the producers. • The green world hypothesis proposed that predators keep herbivore populations in check so that they don’t consume all the plants.	• Prior to the 1960s, what did people think controlled the number of herbivores in a food web? • What was missing from this “bottom up” explanation? • Describe how the green world hypothesis differs from the bottom-up explanation.
3	4:06	7:05	• Robert Paine tested the green world hypothesis on the rocky coast of the Pacific Ocean. He created a food web for the community and then removed the predator, *Pisastor ochraceus*, a starfish, from one outcrop. • Paine discovered that one predator could regulate the composition of an entire community.	• Why was it important for Paine to record the number of different species as well as the overall number of animals on the rock outcrop? • What happened to the number of different species over time? • What conclusion did Paine arrive at after seven years?
4	7:06	8:44	• Keystone species are species in a food web that have large direct and indirect effects on the abundance and number of species in an ecosystem. • Keystone species are often apex predators and are instrumental in maintaining the structure of an ecosystem. • Some species have little influence on the distribution and abundance of other species.	• Why is the arch shape and the keystone at the top of the arch a fitting analogy for what Robert Paine observed? • What does he mean by his claim that some species are more equal than others? • What evidence does he have to support that claim?
5	8:45	11:11	• Paine noted another pattern in tide pools: some had kelp while others didn’t. Those with sea urchins had less kelp. • Paine experimented by removing the sea urchin, and kelp started growing. • The urchins (herbivores) were keeping the kelp (producer) population down to very low levels.	• Why was it important for him to remove urchins from some tide pools but not all others? • How did the observation that sea urchins were eating all the kelp in some tide pools violate predictions from the green world hypothesis?
6	11:12	14:50	• To further explore the impact of predators on other species, Paine and Jim Estes counted the number of urchins and kelp at sites in the Aleutian Archipelago in Alaska in areas with and	• How did the two islands with and without otters differ in the amount of kelp?

			without otters. Sites without otters had lots of urchins and little kelp. Sites with otters had few urchins but lots of kelp. The otters were indirectly controlling the amount of kelp. • A trophic cascade occurs when removal of one species (usually a predator) affects the abundance and distribution of species that it does not directly prey upon.	• How did Payne and Estes' observations support the green world hypothesis? • What were the indirect effects of the removal of sea otters that Paine described? • What is a trophic cascade, and why is it important to understand the relationships it's describing?
7	14:51	18:53	• When orcas started to eat sea otters, it caused a further trophic cascade. Sea otter numbers decreased, urchin populations increased, and the amount of kelp decreased. • Trophic cascades and keystone species have been identified in many other habitats. Understanding top-down effects gives conservationists and scientists a new way of looking at the management of ecosystems with an emphasis on the critical role of apex predators.	• How had human activity influenced the trophic cascade of the Aleutian Islands kelp forest? • Why are apex predators critical to ecosystem structure?

BACKGROUND

THE GREEN WORLD HYPOTHESIS AND KEYSTONE SPECIES

Historically, ecologists had emphasized the importance of "bottom-up" forces on community structure. In this view, the amount and availability of vegetation (primary production) controls herbivore numbers, which then determine predator population sizes. A new approach, called the green world or HSS hypothesis (after ecologists Nelson Hairston, Fred Smith, and Lawrence Slobodkin, who proposed it in 1960), flipped this idea: in some ecosystems, predators control herbivore populations, indirectly supporting plant communities and keeping the world visibly green.

Robert Paine was one of the first scientists to test the green world hypothesis experimentally at the ecosystem level. In the 1960s, Paine designed experiments in which he removed all individuals of the starfish species *Pisaster ochraceus*, a predator, from experimental plots along the Pacific Northwest coast. At the start of his experiment, mussels (*Mytilus californianus*), one of the main food resources of the starfish, covered between 1% and 5% of the rockface habitat, and shared the habitat with 17 other species. However, just three years after the starfish had been removed, only seven species were left on the experimental plots and the mussels covered most of the area. Without the starfish, the mussels crowded out many other species and almost completely displaced four species of algae, a major component of the vegetation of this coastal marine ecosystem. The loss of algae then led to a reduction in other species.

By the end of the study in 1973, the plots without starfish (experimental) were "essentially a monoculture," according to Paine, with mussels covering the rockface, whereas in the control plots the total number of species had remained stable. Thus, removing *Pisaster* starfish allowed mussels to quickly dominate the rockfaces, which in turn drove down the diversity (i.e., the number and distribution of species) of the entire ecosystem.

Students may wonder what the mussels are eating if all other species are gone. Mussels are what's known as filter feeders that live on rockfaces. They feed on plankton from the ocean that floats in when the tide rises.

In 1969, Paine wrote about the findings in a letter to the editor of the journal *The American Naturalist*, in which he introduced the concept of a keystone species. He explained that "[t]hese individual populations [of starfish] are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundances."

Inspired by Paine's unprecedented results, many ecologists in the 1970s began studying keystone species and predators and further testing the green world hypothesis. For example, James Estes and John Palmisano demonstrated that sea otters are a keystone species in the North Pacific coastal ecosystems. In 1975, Estes and Palmisano observed that in areas where otters were rare, sea urchin populations increased in number. The urchins became so common that they devastated the kelp forests, overgrazing the very vegetation that sustains their populations. However, in areas where the otter populations had rebounded, the otters suppressed the urchins and enabled kelp forests to recover. These results show that the sea otters are thus indirectly supporting the kelp forests by regulating the urchins, which feed on the kelp.

THE TROPHIC CASCADE HYPOTHESIS

In 1979, Paine combined his own results with those of others, including Estes and Palmisano, to propose the idea of trophic cascades, in which direct and indirect effects from a species at or near the top of the food chain propagate down and regulate the species and population sizes in the rest of the community.

Research continued and by the 1990s it was clear that the trophic cascade was a real and measurable phenomenon. It also became clear that trophic cascades can change as ecosystems change. As Estes continued to monitor the otter-urchin-kelp food chain through the 1990s, he discovered that killer whales had started feeding on otters. Estes argued that collapses in the killer whale's normal food sources (including Steller sea lions and harbor seals) in the 1970s and 1980s caused this shift in predation. As sea otter populations declined, sea urchin numbers soared, and the kelp forest ecosystem again suffered.

Estes and his colleagues published a summary of their observations, shown in Figure 1, in the journal *Science* in 1998.

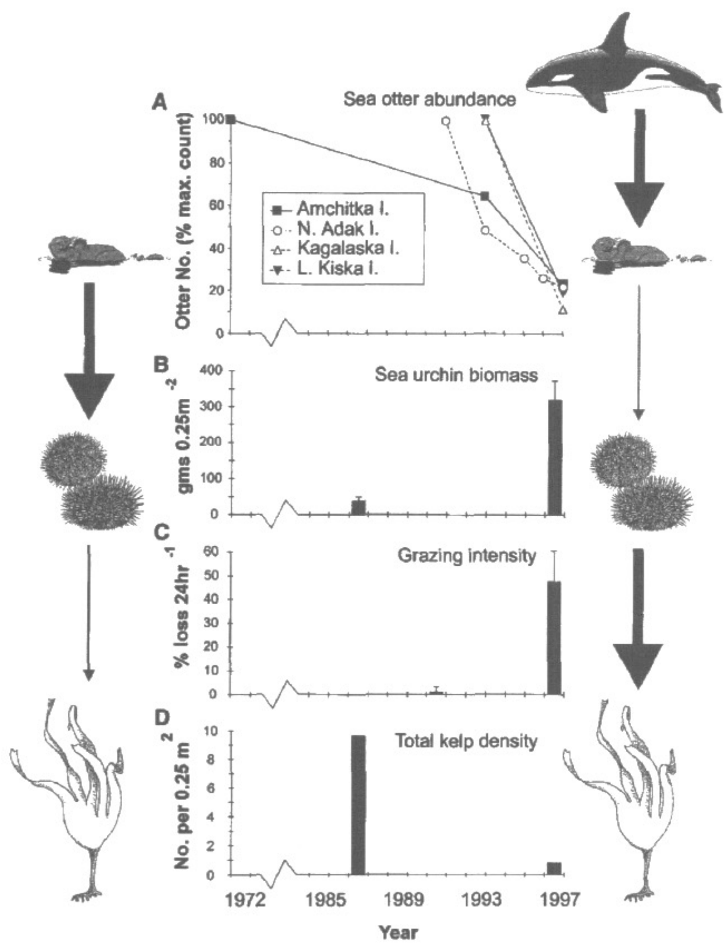

Figure 1. In the kelp ecosystems of the North Pacific, the presence of sea otters in the 1970s and 1980s depressed sea urchin populations and allowed the kelp forests to grow. Killer whales began feeding on sea otters in 1990 in four different monitored locations. Killer whale predation drove down the sea otter populations, releasing pressure on the sea urchin populations, which in turn were able to increase their population sizes and significantly reduce the density of the kelp forests. (Reproduced with permission from Estes, J. A., *et al. Science* 282:473-476, 1998.)

DISCUSSION POINTS

- Students may ask whether keystone species are always apex predators. Apex predators and keystone species are not necessarily the same. An apex predator is a species that sits at the very top of its food web; nothing eats an apex predator. Many apex predators are keystone species, but not all. In the film we learn that sea otters are the keystone species in their food web, but killer whales are the apex predator. Some keystone species, such as African elephants and beavers, are not predators.
- Students may be confused about the difference between bottom-up versus top-down regulation. Stress that both types of regulation play a role in determining the number of species and population sizes, it's not just one or the other. Emphasize to the students that, beginning in the 1920s with Charles Elton's food webs, food pyramids, and trophic levels, ecologists focused on a bottom-up view of biological community regulation: the abundance of primary producers (commonly plants) determined the number of herbivores and hence carnivores. However, Robert Paine and others demonstrated that community structure is also regulated from the top down. The presence or absence of certain species—keystone species—can directly control the populations of some species and indirectly control the populations of other species. In some ecosystems, one type of effect—either top-down or bottom-up—may be more important than the other, and interactions within the ecosystems affect the strength of a particular effect.
- Students may wonder why Robert Paine's work is considered so groundbreaking. Up until the period when Paine performed his starfish experiments, the science of ecology consisted mainly of studies that included census work and behavioral observation. For over 200 years, ecology was almost exclusively a descriptive science, and scientists studying ecology were often referred to as naturalists. Naturalists were mostly interested in describing the natural history of species and determining their distributions and associations with other species. Paine contributed to the transition of ecology to a science based on manipulative experiments.
- In the film we learn about another experiment that Robert Paine conducted by removing sea urchins from their habitats to see what effect they were having on kelp. Based on his experiment and research by Estes and Palmisano, Paine realized that the urchins would consume most of the kelp, their primary plant food source, if their predators (the sea otters) were gone. Ask students if they can think of other examples where humans have removed predators from an area and describe what, if any, effects predator removal has had on the local plant and animal communities. For example, the removal of predators like wolves and mountain lions has led to an increase in whitetail deer populations in North America, which can have a large impact on plant communities.
- Students may be under the impression that trophic interactions are simple and isolated. Make it clear to students that in order to understand the more complex nature of food webs, we must first isolate small parts of them, a three- or four-member food chain, for example, and perform controlled experiments. However, these simple food webs are part of much larger and more complex webs of interactions. Many classic food web studies were purposefully conducted in areas with limited species richness, such as the Arctic or remote islands, to simplify the experiments.
- Students may have been taught the concept of "dominant species" and may be confused about the difference between dominant and keystone species. Explain that dominant species, like the mussels in Robert Paine's experiments, are numerically abundant in their ecological communities. However, removing them may not have much of an effect on community structure other than allowing a similar species to increase in abundance and fill a similar niche. On the other hand, a keystone species is not usually abundant in its community, but as we saw with the sea stars, removing a keystone species can significantly affect the density and presence or absence of most other species in the community.

- Students may wonder how trophic cascades are related to the carrying capacity of an ecosystem for a particular population of a species. The carrying capacity of an ecosystem for a population is influenced by a variety of factors. They include available food resources, water, space, and ecological conditions. If predation is eliminated, as by removing the starfish, the carrying capacity of an ecosystem for a particular population can increase and allow that population to increase, as happened with the mussels, which in turn outcompeted other species.
- What's in a name: starfish or sea star? Echinoderms in the class Asteroidea are commonly referred to as starfish or sea stars. While the term starfish is used in the film, some educators prefer the term sea star to emphasize that these animals are not fish; they are more closely related to other echinoderms like sea urchins and sea cucumbers. This point highlights the confusion that can arise from the use of common names instead of taxonomic and binomial names.
- The film touches on the difference between experimental science and observational science. In experimental science, treatments are used to directly manipulate some aspect of the system, such as the removal of starfish or the addition of nitrogen fertilizer to a field. In observational science, careful monitoring is used to try to understand the responsible mechanisms, but no direct interventions are made. For example, scientists recording climate-induced changes in plant flowering dates are conducting an observational study. When feasible, scientists prefer experimental studies, as this makes it easier to narrow down which variables are responsible for a particular effect. In climate-change studies, this can be accomplished, for example, by a researcher adding CO_2 directly to some plots of plants and testing the influence of high CO_2 levels compared to control plots.
- Stress to students that Paine's and Estes' experiments addressed several classic questions in ecology: What determines how many species live in a location? How big will their populations grow? These experiments supported possible mechanisms but by no means finished answering the questions, and research on these questions continues today.

STUDENT HANDOUT

We designed the student handout as a learning assessment that probes students' understanding of the key concepts addressed in the film, which can be used before or during the film to assess students' prior knowledge and to guide students as they watch the film. We encourage you to choose the use that best fits your learning objectives and your students' needs. Moreover, because the vocabulary and concepts are complex, we encourage you to modify the handout as needed (e.g., reducing the number of questions, explanations of complicated vocabulary for English learner students).

ANSWERS

1. (Key Concepts A & B) True/False. All members of a food web are equal in abundance and in their relative effects on one another.
   False. Some members of a food web can have effects that are disproportionate to their abundance. For example, keystone species have small populations, but because of what and how much they consume, their absence from the food web could have very large effects on the structure of the ecosystem.
2. (Key Concepts A & B) Explain the reasoning or evidence you used to answer Question 1.
   After watching the film, students should realize that some species, like the starfish in Robert Paine's first experiment, which were not as abundant as some other species, can have large effects on the structure of their ecosystems. When the starfish were absent, populations of their primary prey species (mussels) increased so quickly that they crowded out nearly all of the other species in the ecosystem. Students may also mention evidence from the presence or absence of sea otters in the kelp-urchin-sea otter food chains.

3. (Key Concept C) True/False. Every member of a food web is the prey of another member of the food web.
   False. Apex predators are at the top of food webs and do not have predators.

4. (Key Concept C) Explain the reasoning or evidence you used to answer Question 3.
   The diagram of the food chain in the film shows that the starfish is the top predator and does not itself have predators in the tide pools. Also, the film does not explain this, but the orcas don't have any predators either. Their populations are regulated from the bottom up by the availability of food.

5. (Key Concept D) Which statement below explains why the mussels in Mukkaw Bay were able to quickly cover the rockface in Paine's experiment?
   a. The starfish took up most of the room on the rocks, and when the starfish were removed, the mussels occupied the empty spaces.
   b. Paine added more mussels to the rocks, causing the starfish to move to other habitats.
   c. The starfish were competing directly with the mussels for food, and removing the starfish allowed the mussels more access to the food.
   d. Starfish feed on mussels, so when the starfish were removed the mussels no longer had a predator and their populations grew unchecked.

6. (Key Concepts E & F) In the film, Paine recalls that a year after the starfish had been removed, the number of species decreased from 15 to eight, after three years the number went down to seven, and after another seven years it was almost all mussels. In the control plots the number and diversity of species was basically unchanged. Which statement(s) best explain(s) these results?

   I. Keystone species are critical to the diversity and stability of an ecosystem.
   II. When a predator is removed, the prey of that predator always increases and species not eaten by the predator always decrease.
   III. The disappearance of producers from an ecosystem can cause the number of predators to increase.

   a. I only
   b. I and II only
   c. II and III only
   d. I, II, and III

7. (Key Concepts D & F) Before the 1960s, most ecologists thought that the number of producers in an ecosystem was the only variable that limits the number of herbivores. The idea was that every level was regulated by the amount of food from the trophic level below it.
   a. How did the green world hypothesis differ from this "bottom-up" view? ***The green world hypothesis explained that the number of herbivores is also limited by predators from the top down.***
   b. Imagine a simple food chain: Grass -> Grasshoppers -> Mice. If snakes that eat mice are added to this ecosystem, how would you redraw the food chain to represent this change?

      Grass -> Grasshoppers -> Mice -> Snakes

   c. After the snakes are added, would you expect the amount of grass to increase or decrease? Explain your reasoning. ***Answers will vary, but students should expect the amount of grass to decrease. The snakes will cause a reduction in mouse populations, leading to an increase in grasshoppers that will then eat the grass.***

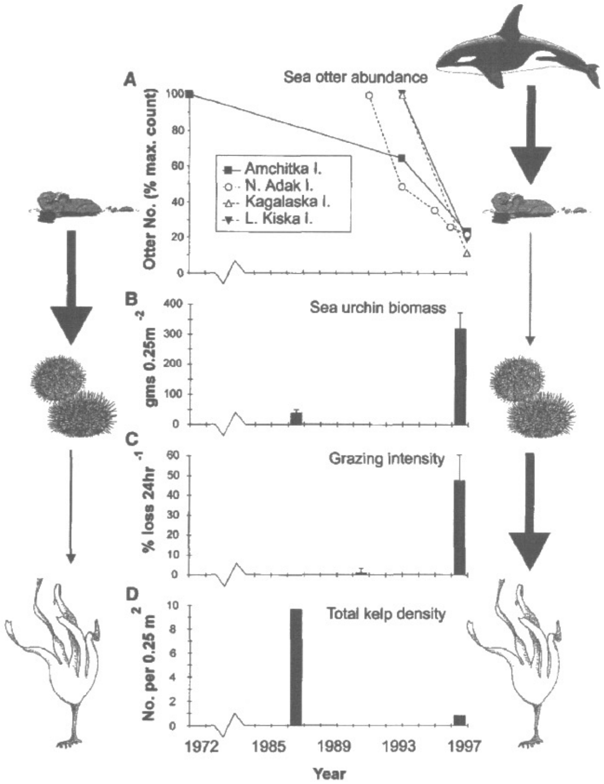

Figure 1. Since 1972, Dr. Jim Estes had been studying a food chain of kelp -> urchins -> sea otters, and then in the early 1990s orcas began eating the sea otters. The data collected by Dr. Estes are shown. Panel A shows sea otter abundance around four different islands from 1972 to 1997. Panel B shows the amount of sea urchins (sea urchin biomass) in 1987 and 1997. Panel C shows the amount of kelp that sea urchins ate over a 24-hour period (grazing intensity) in 1991 and 1997. Panel D shows the number of kelp plants within a specific area (density of kelp) in 1987 and 1997. The thickness of the arrows illustrates the strength of the effect one species has on the species below it in the food web. (Reproduced with permission from Estes, J. A., *et al*. *Science* 282:473-476, 1998.)

Refer to Figure 1 for questions 8 through 11 below.

8. (Key Concepts A & C) In 1997, which species is the apex predator in the food chain?
   a. Killer whales
   b. Sea otters
   c. Sea urchins
   d. Kelp

9. (Key Concepts D & F) Which of the following statements describes the data in Figure 1?
   a. An increase in sea urchin biomass is associated with more intense grazing.
   b. An increase in sea urchin biomass is associated with greater kelp density.
   c. Predation of sea otters by killer whales is associated with greater kelp density.
   d. Sea otter abundance was relatively stable from 1972 to 1997.

10. (Key Concepts D & F) Complete the following sentence. Figure 1 illustrates that when orcas started eating sea otters, the sea otter population ____________________, the urchin population _______________________, and the kelp population _______________________________.
    a. decreased, decreased, decreased
    b. decreased, increased, decreased
    c. increased, decreased, increased
    d. increased, increased, increased

11. (Key Concepts A, C, & D) The arrows on the left and right sides of Figure 1 show the effects of one species on the species that are on lower trophic levels. Thicker arrows indicate a large effect and thin arrows a smaller effect. The arrows on the left show a system in which there are a lot of sea otters. The arrows on the right show a system in which there are few otters. Explain why the down-pointing arrows on the left side of the figure look different from the arrows on the right side of the figure.

On the left, the sea otters have a large effect on the sea urchins in the absence of the killer whales. The sea urchins have a small effect on the kelp because their numbers are held in check by the sea otters. On the right, the killer whales have a large effect on the sea otters, whose populations then decrease. The effect the sea otters have on the sea urchins is thus weaker, allowing sea urchin populations to grow, and they in turn have a large effect on the kelp.

In the 1990s, ecologists Deborah Letourneau and Lee Dyer studied a tropical forest shrub called the piper plant and the various species of insects that live on and near the shrub. A species of ant uses the piper plant as a home by hollowing out some of its branches and building colonies inside the hollow branch cores. The ants do not eat the plant's leaves. Instead, the leaves are consumed mostly by caterpillars. When the ants encounter caterpillars or caterpillar eggs on the plant's leaves, they either eat them or kick them off. Letourneau and Dyer added beetles that eat ants to some plants and then measured their effect. Figure 2 shows the results of one of Letourneau and Dyer's experiments in which they compared the leaf area of piper plants in control plots to that of experimental plots to which they had added beetles that eat ants.

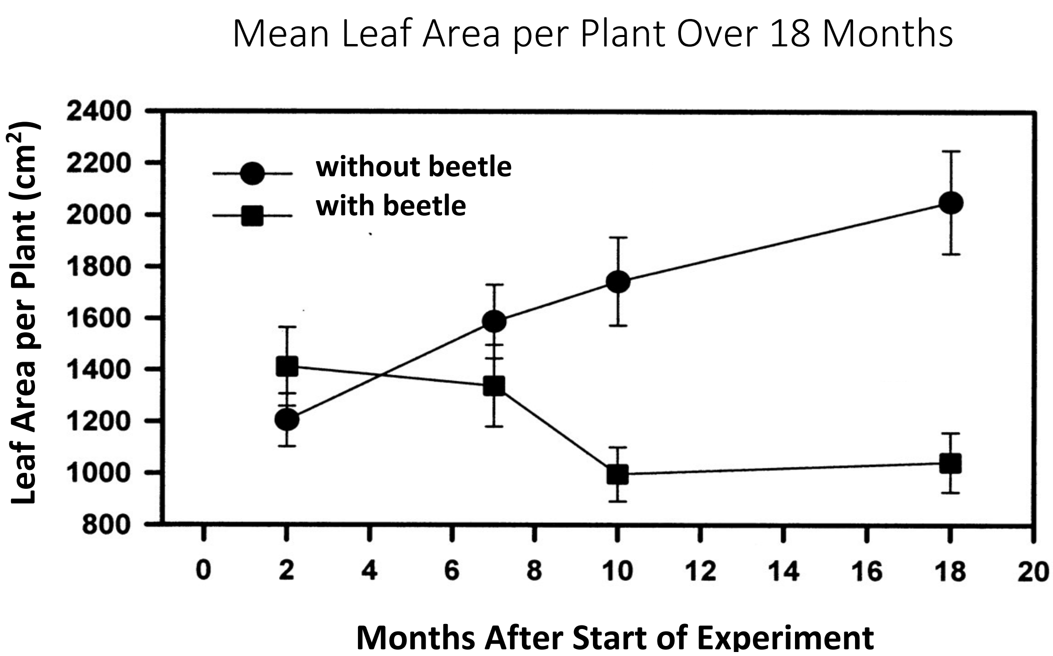

Figure 2. Mean leaf area per tree. Initial measurements were taken before (0 to 2 months) and after (7 to 18 months) beetles were added to 40 of 80 plants. The light gray round markers represent measurements taken of the control plots, to which beetles were not added. The black square markers represent measurements taken of the experimental plots, to which beetles were added. Measurements were made on all leaves to calculate the mean leaf area per plant. Error bars represent standard error of the mean.

Refer to Figure 2 to answer questions 12 through 17.

12. (Key Concept F) For both the plots with the beetles added and the control plots (no beetles added), estimate the mean tree leaf area per plot that the scientists recorded after running the experiment for 18 months.

    Students should answer about 2,000 cm^2 for the control plots and 1,100 cm^2 for the plots with the beetles added.

13. (Key Concept F) Compare the trends in mean tree leaf area per plot for both the plots with the beetles added and the control plots over the 18 months of the experiment.

    Students should describe that the leaf area for the control plots without beetles increased over the 18-month period, but decreased for the plots where the beetle larvae were added. A complete answer will be one in which students also explain that the mean leaf areas were similar through about the first 7 months of the experiment but after that, the differences between the means may be significant. (A statistical test, like the student's t-test, is needed to determine whether the difference is indeed statistically significant.)

14. (Key Concepts D & F) Draw two diagrams that show the food chains for the control and experimental plots. Include interactions among predatory beetles (if present), ants, caterpillars, and piper plants.

Control	Experimental
piper plants → caterpillars → ants	*piper plants → caterpillars → ants → beetles*

15. (Key Concepts D & F) Describe the impact of adding the beetles on each species in the food chain above.
The beetles eat the ants. With fewer ants there are more caterpillars. The caterpillars eat more leaves.

16. (Key Concepts D & G) Which statement do Letourneau and Dyer's results support?
    a. Adding beetles reduced ant numbers and triggered a trophic cascade that increased the mean leaf area left on plants.
    b. Adding beetles had little effect on this ecosystem, showing that it is primarily regulated from the bottom up.
    c. Adding beetles reduced ant numbers and triggered a trophic cascade that decreased the mean leaf area left on plants.
    d. Adding beetles reduced ant numbers and increased the caterpillar population size, proving that the caterpillars are a keystone species in this habitat.

17. (Key Concept D) Do the results of the Letourneau and Dyer experiment support or refute the green world hypothesis? Explain your answer.
The experiment supports the green world hypothesis because changes in plant leaf area were caused by predators controlling herbivore numbers from the top down. Adding beetles decreased ant predation on caterpillars and led to increased caterpillar herbivory and decreased plant leaf area.

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