The Wolf, the Moose, and the Fir Tree: A Case Study of Trophic Interactions

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Part I – Introduction

Isle Royale National Park, the largest island in Lake Superior, provides biologists with a fairly unique system for studying the interactions between different trophic levels. Isle Royale has a rather simple food chain consisting of producers and a single large herbivore that in turn has only a single predator, the gray wolf *(Canis lupus).* The island had a rather large abundance of balsam fir *(Abies balsamea)* until the park was colonized by moose *(Alces alces)* that swam to the island in the early 1900s. After the establishment of this large herbivore, the balsam fir declined from 46% of the overstory in the 19th century to about 5% today. Nearby islands that are inaccessible to moose continue to have a large fir component in their forests; thus the decline of the fir on Isle Royale has been attributed to moose herbivory. Balsam fir is not considered optimal forage for moose but it can comprise up to 59% of their winter diet.

Over the last several decades, significant temporal fluctuations have been observed in the densities of the wolf and moose populations and the growth rates of balsam firs. Two hypotheses have been suggested to account for these fluctuations. The primary productivity or "bottom up" hypothesis suggests that plant growth is limited by the energy available to plants, which is determined in turn by temperature and precipitation. Additional plant growth means more forage is available—thus herbivores, and ultimately carnivores, should increase in abundance. Alternatively, the trophic cascade or "top down" model predicts that changes in one trophic level are caused by opposite changes in the trophic level immediately above it. For example, a decrease in moose abundance should produce increased plant growth if moose herbivory limits plant growth. Changes in primary productivity would only have a discernible effect on vegetation if higher level interactions had been removed.

The Isle Royale ecosystem provides us with a good opportunity to test the predictions of these alternative hypotheses. Longitudinal data are available for each of the key variables, including annual plant growth, herbivore density, and carnivore density. The historical growth rates of balsam fir have been determined through tree-ring analysis. When herbivores remove large quantities of the foliar biomass, annual wood accrual decreases and ring widths are reduced. Thus tree ring data allow us to estimate the intensity of herbivory over time. Moose and wolf populations have been censused for decades on Isle Royale, providing us with annual estimates of herbivore and carnivore densities. Long-term records are available for each trophic level in the Isle Royale ecosystem, providing the necessary data to evaluate both hypotheses.

Questions

1. What type of correlation (positive or negative) would you expect to see between the population densities or growth rates of each trophic level in this system (fir/moose/wolves) under the primary productivity hypothesis?
2. What type of correlations would you predict under the trophic cascade hypothesis?
3. What would you predict as the effect of wolf removal on plant growth under each hypothesis?
4. What assumptions are made regarding the measurement of growth rates in balsam fir? Regarding the long-term impact of moose herbivory on balsam fir? Do these assumptions seem warranted?

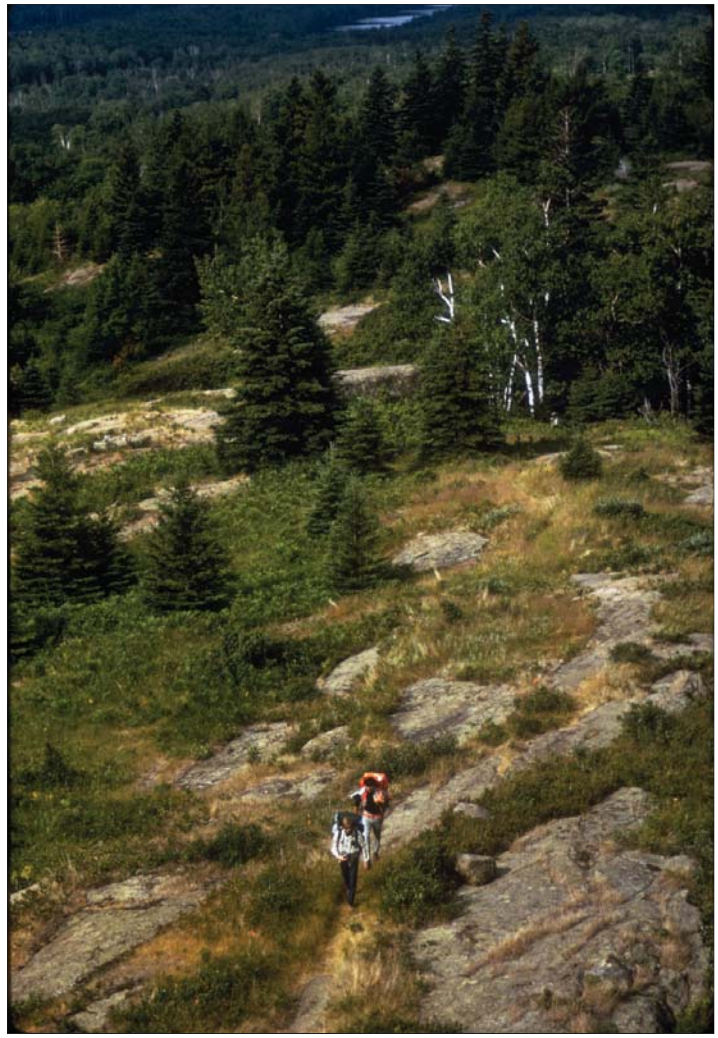

Photo credits: Wolf *(Canis lupus)* by Gary Kramer, U.S. Fish and Wildlife Service, public domain. Swimming moose and hikers in Isle Royale National Park are from the National Park Service Digital Image Archives, public domain.

Part II – Trophic System Data

The data in Figure 1 include census information for the moose and wolf populations, ring width indices from firs on each end of the island, and actual evapotranspiration rates (AET) from April to October. The east and west ends of the island differ substantially in terms of climate and flora. The west end consists of hardwood forests with a higher AET rate and warmer, earlier summers relative to the boreal forests in the east. The AET rate varies with temperature and rainfall and serves as an index of the amount of water available for plant growth. This rate is strongly tied to primary productivity.

Questions

1. What is the purpose of each figure? Are there unclear terms or confusing aspects to any figure?
2. How do the maxima and minima of the ring-width indices correspond to changes in moose density? Does this support the primary productivity hypothesis, the trophic cascade hypothesis, or neither?
3. Do firs from either end of the island (east/west) respond the same way to changes in moose density? How can you account for any observed differences?
4. How do the maxima and minima of the wolves correspond to changes in moose density? How might you account for this relationship?
5. Which hypothesis is supported by the data on annual AET?

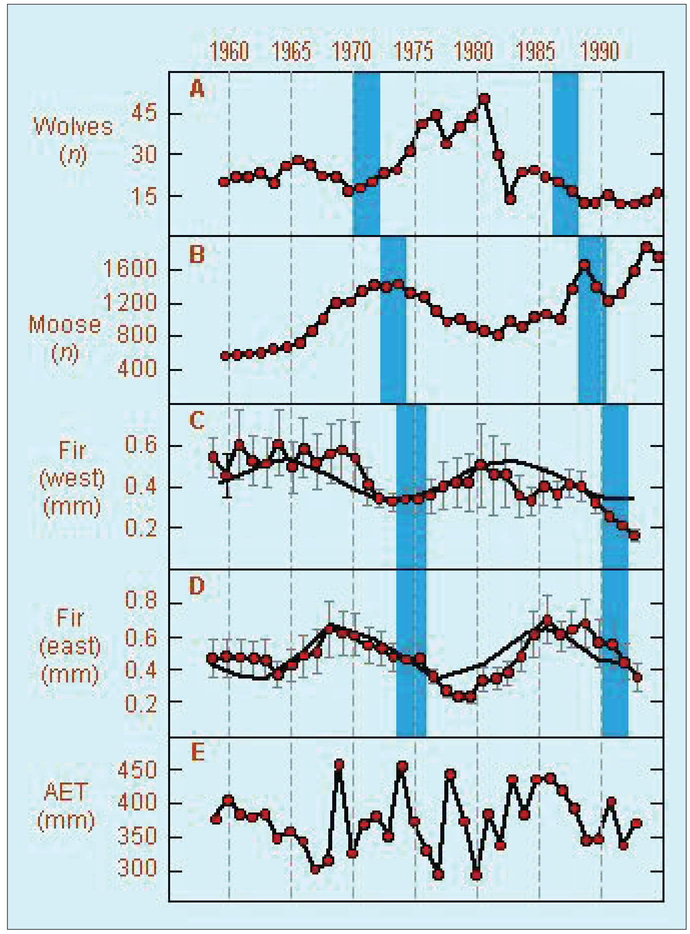

Fig. 1. Population parameters of the Isle Royale ecosystem from 1958–1994. Shaded areas signify periods of forage suppression that may be connected to interactions between herbivores and carnivores.

A. Population size of wolves each winter (based on aerial counts).

B. Population size of moose each winter (based on aerial counts and skeletal remains).

C. Ring-widths from the west end of Isle Royale, N=8.

D. Ring-widths from the east end of Isle Royale, N=8.

E. Actual evapotranspiration rates (AET), annual calculations based on data from April–October at a weather station 20 km from Isle Royale. AET is an approximation of primary productivity, it represents water availability as a function of temperature and rainfall.

Credit: Regraphed from information published in *Science* 226 (December 2, 1994): 1557.

Part III – Ring Width Indices

The local topographies for the two samples depicted below are substantially different. The chronologies in figure A are from an east-end subsample of trees designated RH (Rock Harbor). This area contained an open-canopy section of previously disturbed boreal forest; it exhibits an increase in growth rates after a period of high wolf predation in the late 1970s. Figure B depicts a west-end subsample designated SS (Siskiwit Swamp). These firs are in a closed-canopy hardwood forest that has been heavily browsed by moose for some time.

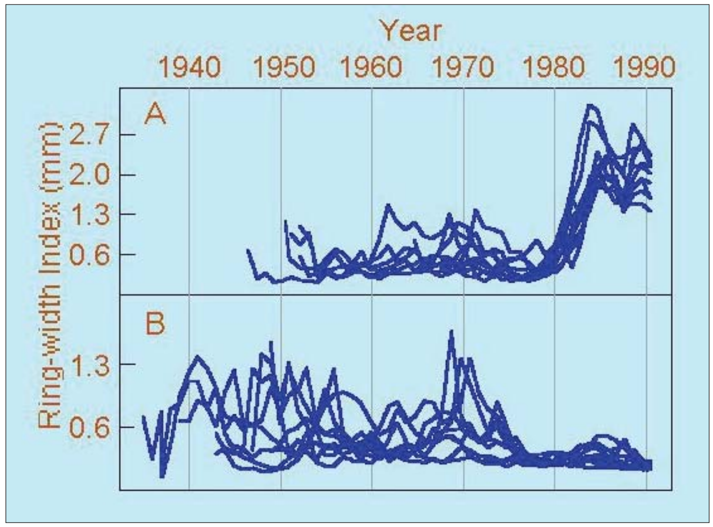

Fig. 2. Ring-widths of balsam firs from Isle Royale. Each line represents data from an individual tree harvested in 1992. Note that moose are able to browse as high as 3m.

A. Location RH (N=10), firs from this area were 26–48 years old and exceeded 3m in height during the late 1970s.

B. Location SS (N=9), firs from this area were 48–60 years old and were less than 2m in height.

Credit: Regraphed from information published in *Science* 226 (December 2, 1994): 1557.

Questions

1. Are there any confusing aspects to the figures or caption above?
2. The moose population peaked in the mid 1970s and then declined over the next decade. How did the trees at each site respond in the years following the peak? Are the results for these samples surprising given the larger data sets for tree ring-width on the previous page?
3. How should the difference in canopy cover affect growth rates? How will the height of the trees at each site affect their response to changes in primary productivity? The authors suggest that primary productivity was increasing during the late 1970s and most of the 1980s—does either ring-width index appear to reflect that change?
4. Which hypothesis do you feel is best supported by the ring-width chronologies above?
5. What final conclusions can you draw about the interactions between each trophic level on Isle Royale? Is control exerted from the top down, as suggested by the trophic cascade model, or are interactions between trophic levels ultimately controlled by primary productivity?
6. Design an experiment that would allow you to clarify any ambiguities from Figures 1 or 2. Why might an experimental approach prove advantageous in this situation?