Carrying Capacity
and Limiting Factors

This document addresses carrying capacities and limiting factors. Imagine our planet as a global bus. If a bus has enough seats for fifty passengers, we would all agree that we could crowd a few extra persons on board in an emergency. But *how many* extras could the vehicle accommodate? What if 291 passengers climb aboard, or 937, or 7428?

Clearly, at some point, a critical system would fail. The engine would overheat, the tires would blow, the axles would break, the transmission would fail, or the engine would blow a gasket. In all likelihood, the first system to be affected by crowding would be the restroom at the back of the bus which would overflow as the amount of waste generated by the passengers overwhelmed its capacity to accommodate those wastes.

Why should we suppose that the earth's
environmental machinery is invulnerable?

Carrying Capacity

How many organisms can a particular ecosystem [or planet] support over a long period of time without suffering severe or irreparable damage? To scientists, the answer to such a question constitutes the system's carrying capacity. Since ecosystems are finite in their size and resources, each has an upper limit to the population that it can support. In other words, each system has an upper limit to its ability to provide food, resources, maintain itself, resist damage, and provide the assorted ecological services that allow a given population to exist.

Hardin (1986) likens carrying capacity to an “engineer's…estimate of the carrying capacity of a bridge." Biologists also sometimes use the term "thresholds" to refer to limits that, when exceeded, constitute critical boundaries within a system. As Soule (1985) observes, "Many, if not all, ecological processes have thresholds…." In the same paper, Soule reminds us that "genetic and demographic processes" also have thresholds (ibid).

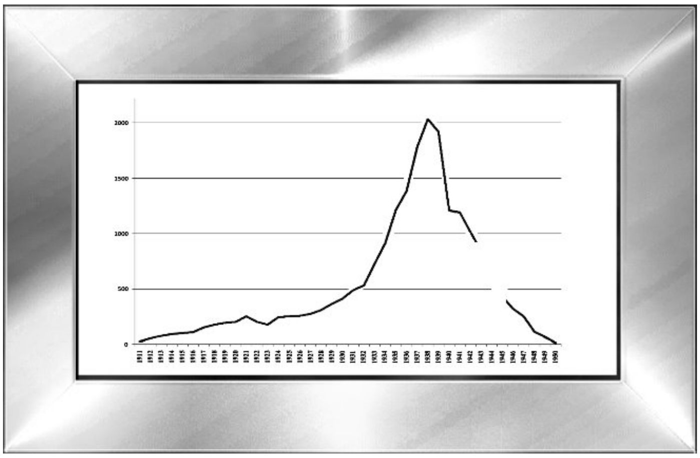
In this excerpt and throughout **Wecskaop**, we are addressing earth's carrying capacity for our own species. What happens if an animal population exceeds its carrying capacity? What factors limit a population's ultimate size?

In his book HOW MANY PEOPLE CAN THE EARTH SUPPORT? (1995), Joel Cohen points out that we have moved into "...a poorly charted zone where limits...have been anticipated and may be encountered." More recently we see that despite recently slowing population growth in the world's rich and most technologically advanced countries, "the historically unprecedented population expansion in the poorest parts of the world continues largely unabated" and "as a consequence, nearly all future global growth will be concentrated in the developing countries, where four-fifths of the world's population lives" (Bongaarts, 2002).

Exceeding Carrying Capacities

In a classic study of a “boom-and-bust” population explosion Scheffer (1951) followed a population of reindeer on St. Paul Island, Alaska from 1910 to 1948.

The Rise and Fall of a Reindeer Herd
on St. Paul Island, Alaska

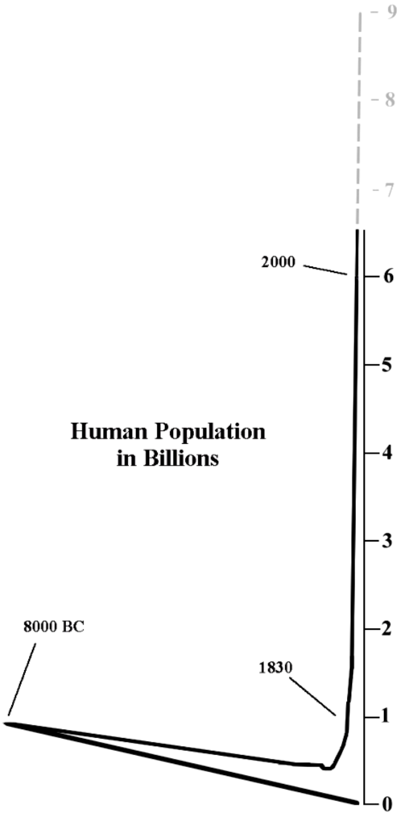


The 40 square mile island had no wolves, predators, or major competitors for the reindeer in the study. Notice the rising trajectory of the curve produced as the population grew over the years. Secondly, however, notice the collapse underscored by the last data point in the graph in which a 99% die-off took place. Thirdly, the reindeer occupied less than one tenth of one percent of the area theoretically available to them at the time of the collapse so that the die-off took place even as vast “amounts of open space” still remained. We will encounter this and similar patterns throughout this book. (No data were able to be collected during World War II.)

Graph is after Scheffer, V.B. 1951. *The rise and fall of a reindeer herd.* Scientific Monthly 73: 356-362.

The island had no wolves, predators, or major competitors so that the reindeer population exhibited approximately 28 years of relatively unrestricted and unfettered growth. The herd’s initial phase of exponential growth, however, was followed by a catastrophic die-off or collapse in which 99% of the herd died out by the close of the study in 1948. It is important to recognize that the reindeer **occupied less than one-tenth of one percent** of the area that remained theoretically-available to them at the time of the collapse so that the die-off took place even as “vast amounts of open space” remained.

In a follow-up study to test Scheffer’s results, a second small reindeer population was introduced to Alaska’s St. Matthew Island under much the same conditions. When Klein (1968) reported on the fate of this second herd, the results were similar – and equally shocking. Initially, Klein’s herd grew exponentially until it underwent an even more precipitous collapse in which 99% of the reindeer died over a one year period.



<u>Perhaps the most disconcerting aspect of these two studies is the following</u>:

A graph that traces our own population growth over the past ten millennia not only mimics the pattern seen in the climb-and-collapse of the two reindeer herds, but notice that our own pattern of growth (as shown left) is both *more pronounced and far more extreme* than that seen in the reindeer herds as they neared collapse.

In fact, our graph (and the numerical progression that it depicts) actually ***surpasses*** the already-overwhelming pattern of growth that characterizes a typical "exponential" progression, prompting biologists to classify such ultra forms of exponential progessions as **hyper**exponential (e.g., Cohen, 1995).

Limiting Factors

Scientists recognize a variety of limiting factors that play a role in regulating the ultimate size of a population in a given environment. And while finite supplies of critical resources such as food and water are sometimes important, *they are* not *the only factors* that determine a system's carrying capacity.

There are *many* OTHER *important factors*, for instance, that act to limit a population’s size. An example (discussed elsewhere) demonstrates that the <u>absence of wolves, bears, and competing species</u> allowed the reindeer herds in the two Alaskan experiments to grow far beyond the carrying capacities of their environments.

Additionally, as a general rule, as populations become larger and increasingly <u>crowded</u>, increasing **competition** occurs between individuals and between species. Thus, among birds, there may be competition for a limited number of nesting sites, and marine tunicates and sponges may compete for limited attachment sites on a pier piling or offshore rocks. Similarly, ever-larger populations are an invitation to sanitation problems and/or to an increasing likelihood of epidemic disease. (e.g., Odum, 1959).

Still other limiting factors, such as predation, commonly play a critical role in regulating the size of a population. As one example, Paine (1966; 1969) described the role of the predatory sea star, *Pisaster*, in regulating the abundance of various prey species in rocky intertidal marine habitats. A similar pattern is also seen in the role of sea otters that prey upon and thereby regulate, sea urchin populations in California's kelp beds (e.g., Estes and Palmisano, 1974; Duggins, 1980).

Even hormonal, adrenal, and physiological stresses can act as limiting factors. For example, crowded populations often exhibit increases in aggression and infant mortality, along with hormonal and physiological stress responses. Some studies have shown, for instance, that "rabbits, when crowded, exhibit a shock disease...with enlarged adrenals, a breakdown in the adrenopituitary system, and a wholesale die-off" (Christian, 1950, 1956; Christian and Davis, 1964; Calhoun, 1962).

Damaging the Physical Environment

As populations become larger and/or more crowded, they often inflict damaging changes to their physical environment. Each ecosystem has an ability to maintain itself and resist or heal physical damage, but these capabilities have limits. For example, when lakes and ponds undergo **eutrophication**,* they demonstrate damaging changes that are inflicted by the populations that they host.

* Eutrophication constitutes an over-fertilized condition
resulting from fertilizer run-off or animal wastes, etc.

If plants and other autotrophs living in a lake or pond are nourished with abundant nutrients (e.g.-from animal wastes or fertilizers) they respond with a burst of exuberant growth. The problem is, dissolved oxygen levels in the water are limited. Each night at dusk, even though photosynthetic production of oxygen ceases, the crowded and over-abundant populations living in the pond continue *consuming* the limited supply of O_2 all night long.

In this case, heterotrophic microbes utilize the available “O_2 faster than it can be replenished,” resulting in “complete depletion of O_2" (Prescott, 1999). When this happens, the pond or lake becomes **anoxic** (without oxygen), thereby suffocating essentially all aerobic populations in the pond.

Thus, in this case we see calamitous changes that result from too many organisms drawing on a limited resource.*

* *Also notice that the problem here is* not *due*
to limited supplies of food and nutrients.

Instead, in this instance, extra nutrients
actually serve to fuel the growth that leads to depletion of O_2.

Damage to the physical environment can also be inflicted by vertebrate animals like ourselves. We see, for example, that when elephants are confined to small areas, they destroy the very trees and vegetation needed for sustenance. In the same way, when predator populations were reduced near the Grand Canyon in the early 1900s, local deer populations exploded, and began to consume "...every leaf of available vegetation" (Odum, 1959). Nearly everywhere we look and nearly everywhere we travel, we see evidence that our own species is inflicting physical and chemical damage to earth's ecosystems and to our physical, climatic, and biological environments.

A Limited Capacity to Accept Wastes

It is intuitively obvious to most of us that the carrying capacity of a particular environment can be limited by the amount of food and other resources a population requires. However, carrying capacities *can also be limited* by the ability of an environment to accept and process the **wastes** of a given population. For example, in a population of yeast, Gause (1932) cited alcohol's effects on new cells as the limiting factor. Similarly, as Stiling has observed (2002) "It is interesting that in this situation population growth was limited by pollution of the environment by alcohol [and] not by limiting resources." Continuing, he notes that many people "think the same will be true of humans" (ibid).

In the case of humans, of course, the wastes of our bodies, our biological wastes, generally constitute a minimal threat to the earth's environment. On the other hand, the cumulative impacts of our industrial and societal wastes (including chlorofluorocarbons, heavy metals, radioactive nuclear wastes and rising levels of greenhouse gases) represent significant challenges to global systems. As William Catton once observed, we are "already suffering the plight of yeast cells in the wine vat. Accumulation of the noxious and toxic extrametabolites of high-energy industrial civilization [has] become a world problem" (Catton, 1982).

Our point is this: Although it is quite appropriate to consider finite supplies of food, water, and critical resources as factors that limit a species to some ultimate population size, we are guilty of error if we allow those topics to be the only focus of our concern. On a passenger bus, for example, it is easy to recognize a finite supply of available seating as a limiting factor that affects the vehicle's ultimate capacity. But if we were to actually crowd additional passengers onto such a bus, while the seating might become more crowded and increasingly uncomfortable, the vehicle might still lumber forward, even with a load of one hundred or more.

Possible Implications for Us

On the other hand, that restroom at the back of the bus is easy to overlook until actual crowding takes place. Even though the transmission, axles, seating, brakes, and engine might be stressed by one hundred or more passengers, those systems might manage to struggle onward under the load. That restroom, however, might not respond so well. Assuming a long trip, one can imagine overwhelming its capacity by the presence of as few as sixty or seventy passengers.

Upon reflection, we can see that this scenario might apply to earth. <u>If we assess the collective impacts that we have right now, with a population in excess of 6.8 billion, a lot of the stresses we see are the result of our societal and industrial wastes</u>. *Food and other resource shortages may be* *out there on the horizon as looming problems, but earth's ability to accept, recycle, cleanse, and dissipate our avalanche of societal and industrial wastes* (such as CO_2) *appears to be stressed already*.

In their text BIOLOGY (1999), Campbell, Reece, and Mitchell express a similar caution: "It is... possible that our population will eventually be limited by the capacity of the environment to absorb the wastes and other insults imposed by humans." Joel Cohen has made a similar appraisal: "Today's rapid relative and absolute increase in population stretches the productive, absorptive, and recuperative capacities of the earth" (1995). Still others, such as Raven and Johnson (1999), remind us that "the world ecosystem is already under considerable stress."

Thus, if we allow ourselves to focus exclusively on food supplies, which too many previous studies have done (see, for example, Revelle, 1976), we may distract our attention from other critically important aspects of our problem. In his book OVERSHOOT, William Catton wrote: "...the capacity of the world's oceans, continents, and atmosphere to absorb the substances [*Homo sapiens*] must put somewhere in the process of living is limited. Even as a waste [pollution] disposal site, the world is finite" (1982).

“Open Space” – An Erroneous Supposition

When discussing population limits, we are often tempted to suggest that a growing population may eventually "run out of space." We argue here that such appraisals require clear specificity lest they be misleading. The term "space," for example, technically refers to a mathematical area or volume. The resulting problem then, is this: The term carrying capacity does ***not*** refer to the sheer number of individuals whose bodies can be physically squeezed into a given area or volume.

First, among mammals, the two experiments with reindeer herds on Alaskan islands resulted, in each case, in a population explosion that was followed immediately by a catastrophic die-off, (with 99% mortality in both cases). It is also important to note that the die-off in both reindeer populations occurred even when each herd had "vast amounts of open space” remaining at the time of the collapse.

For example, the St. Paul Island herd (see graph at the outset of this document) collapsed even as more than 99.9% of the island remained theoretically available to them. Thus, envisioning quantities of “open space” as a standard by which to judge earth’s carrying capacity for an industrialized humanity constitutes a dangerously mistaken supposition.

To clarify this point further, imagine a national park in Africa and its carrying capacity for lions. Although the enormous measured areas of a large reserve might allow us to physically squeeze hundreds of thousands or even millions of lions into such a park, to sustain even small numbers of lions, there must be vast game herds with populations large enough to allow a *harvestable surplus* of zebra and wildebeest.

These vast game herds, in turn, require even *greater* expanses *of grasslands* to sustain their grazing and seasonal migrations, along with adequate supplies of water. Consequently, hundreds of square kilometers of "open-space" are necessary to support even a small population of lions. Thus, to suppose that millions of lions might occupy a reserve simply because its mathematical dimensions can physically accommodate their bodies would grossly misrepresent biological reality.

It is clear that attachment sites for marine invertebrates such as sponges and bryozoans might, in one sense, be considered "space-limited" resources. And, to establish nature reserves for conservation purposes, expansive quantities of "space" are essential if viable populations are to persist. Soule, for instance, observes that even the largest nature reserves and national parks today "...are usually too small to contain viable populations of large carnivores" (Soule, 1985).

However, the sheer physical dimensions (area or volume) of available space, while necessary, incorporate *other* more-immediate limiting factors that operate and exert their influences within that space. We have already seen, for example, not just intuitively-obvious limiting factors such as supplies of food and water, but also predation, disease, environmental damage, territorial disputes, waste accumulation, aggression, competition between and within species, and some cases of hormonal, physiological, and/or behavioral dysfunction.

Hence, the sheer amount of available "space" is seldom biology's central limiting factor, which means that the apparently "vast open spaces" of the American west or the Australian outback or the Mongolian steppes are largely irrelevant. A yeast population, for instance, poisons its grape juice environment with ethanol while occupying a volumetrically *insignificant* portion of the bottle in which it resides. Similarly, populations of dinoflagellate cells routinely poison hundreds of square kilometers of the sea even as the cells themselves occupy volumetrically insignificant portions of the "space" in which they live.

(See our "Open-space and Climate pdf for an
expansive elaboration on this topic.)

(Additional considerations are also presented in our
"Razor-thin Films" pdf addressing earth's atmosphere and seas)

Likewise, the occupants of a eutrophic (over-fertilized) lake or pond can induce lake-wide **anoxic** conditions (a lethal depletion of dissolved oxygen) even though the actual volume *occupied* by their bodies and cells amounts to an insignificant proportion of the total volume available.

Shoulder to Shoulder

One occasionally encounters blogs or talk show discussions in which a little mathematics is used to suggest that "all the people on our planet could stand shoulder to shoulder in an area the size of Minnesota." While such statements may initially sound persuasive, they are actually founded upon exactly the same fallacious "available open space" ideas that we have just been addressing. Upon reflection, however, (and as our "Open-space" pdf also shows), such statements omit enough key considerations that they render themselves invalid. In order to evaluate such comments, for example, we might begin with a modified version as follows: Suppose someone suggests that, mathematically speaking, we could squeeze all of earth's wildlife populations shoulder to shoulder into a geographic area "X," for argument's sake, the size of Minnesota.

Imagine, then, squeezing every chimpanzee, elephant, buffalo, bird, mountain lion, squirrel, giraffe, orangutan, musk oxen, harbor seal, tarantula, manatee, komodo dragon, cow, tiger, whale, and rhino shoulder to shoulder into an area the size of Minnesota. Even if this could somehow be done in a grotesquely physical sense, it would be absurdly unrealistic to suppose it to have any relationship at all with real-world systems.

First of all, such a scenario leaves no room for the woodlands and forests, or the waters, rivers, streams, grains, food, expansive grasslands, and specialized habitat niches needed to support those populations. Secondly, the scenario leaves no room for the environmental damage and waste products generated by all of those organisms. And thirdly, the ensuing chaos and carnage resulting from movement, competition, aggression, and predator-prey interactions would be unimaginable.

In the same way, statements that imagine crowding all of humanity shoulder to shoulder into geographic area "z" are just as fallacious. Why? Because they ask us to **presume** that the physical "amount of space" constitutes the principle limiting factor affecting our species. To achieve a more realistic appraisal of a carrying capacity, it would be more appropriate to ask how many people can live in Minnesota on a long-term basis (many generations) if they must rely solely on the resources and waste-cleansing capacity of that state alone.

The Global Dashboard

A passenger bus has warning lamps on its dashboard that light up to indicate trouble. On earth today, we already see a disconcerting number of warning lights beginning to light up the global dashboard. Examples of these include accelerating emissions of greenhouse gases, disappearing wilderness, massive deforestation in the tropics, acid precipitation, melting permafrost, collapsing fisheries, falling water tables, desertification, disappearing polar ice, ozone depletion, and an imminent mass extinction that may become the greatest biological disaster since the disappearance of the dinosaurs (e.g., IPCC, 2007; Pimm, 2001, etc.).

If our planet already shows so many signs of stress with our present population of 6.8 billion people, what will happen when that portion of humanity who are not yet industrialized attempt to emulate our own standard of living?

And what will happen if we add the stresses of
additional billions over the next forty years?

How long can earth's biological, climatic, waste-cleansing, and environmental machinery survive the cumulative impacts of our ever-expanding numbers?

We don't know the exact answers to these questions yet,
but children now living are likely to find out.

Other Passengers

We are not alone on our global bus. Other species occupy much of the available seating. Today, however, with billions of additional human passengers boarding, these other species are being displaced at an accelerating rate. By mid-century, for example, "...large species, and particularly large predators, will be by and large extremely scarce and some will have disappeared entirely" (Jenkins, 2003). Continuing, Jenkins adds: "almost all wild lands in the tropics will be impoverished in numbers and diversity of larger animal species" and concludes that continuing loss of forests in Indonesia, Madagascar, and the Philippines will "have a particularly high impact on biodiversity" (ibid). Likewise, Pulitzer Prize winner Thomas Friedman cites a Conservation International estimate that a “forest area the size of three hundred soccer fields is cut down in Indonesia every hour” (Friedman, 2008).

Similarly, Sylvia Mader explains that today "two-thirds of the plant species, 90% of the nonhuman primates, 40% of birds of prey, and 90% of the insects live in the tropics" (Mader, 1996). Continuing, she points out that "every year humans destroy an area of forest equivalent to the size of Oklahoma. At this rate, these forests and the species they contain will disappear completely in just a few more decades" (ibid).

We hear similar concerns expressed by Raven, Evert, and Eichhorn: "As many as 40,000 species of tropical plants may be in danger of extinction in the wild within the next several decades" while "in temperate regions, about five percent of the native plant species are in current danger of extinction" (Raven, et al., 1986). If our own species suffers because of our own actions or inactions, that suffering will be self-inflicted. But what about all the other passengers aboard our bus?

Do other species have a right to exist?
Is it our right to drive them to extinction?

Or does there exist a moral imperative to preserve our
biotic inheritance and the fabric of life on earth?

At the edge of a forest, we see vines that compete with trees for sunlight. In the backyards of our homes, we see squirrels that compete with birds for birdseeds. In Africa, hyenas compete with lions for a carcass. Similar instances of competition exist throughout the natural world. Today, however, humans compete with wildlife for wilderness. And in such a competition, wildlife and wilderness stand no chance.

Today, a hungry, poor, and rapacious humanity – along with the economic engines of our wealthiest societies – lays waste to the natural world at a rate unparalleled in human history. Which, if any, species will survive the holocaust that is now underway? What portion of earth's biota will we drive to extinction in the years just ahead?

WECSKAOP and these PDFs prompt us to
engage such questions and their implications.

Closing Questions and a Recommendation

How far can we push natural systems before they break? How many people can the earth support? At what standard of living? How many should it support? Do other species have a right to exist or should all of earth's resources be used to support humans alone? Do future generations have any rights to resources and raw materials? Or is it the right of generations now living to consume all such materials entirely and leave the poisonous wastes for someone else to clean up later? Do future generations have a right to inherit an intact planet with functioning ecosystems and the biodiversity that we inherited when we arrived? Or is it the right of those of us now living (or of our economic and corporate entities) to consume, pollute, and destroy to the maximum extent possible?

What happens when a population overshoots the carrying capacity of its environment? What evidence will we see when such overshoot has occurred or is occurring? Might humanity be in an overshoot mode already – *right now?* (We are.)

What happens to other species when they overshoot the carrying capacity of their environments? To what extent have our advances in medicine, life extension, public health, and antibiotics suppressed our chief predators, pathogenic microbes, from their role in regulating our populations? Is our species currently undergoing a population phenomenon known as ecological release? What price is to be paid if we continue on our present course?

The National Academy of Sciences should immediately empanel a team to evaluate such questions of overshoot, including the possibility, likelihood, and consequences, in the event that our present overshoot of earth's carrying capacity continues over the half-century ahead. And, in our opinion, the members of the panel should be well-represented by natural scientists specializing in population biology, biology, atmospheric science, zoology, botany, marine science, ecology, and chemistry -- as opposed to demographers, social scientists, economists, and statisticians.

A continuation of today's demographic tidal wave *may constitute*
the greatest single risk that our species has ever undertaken.

Excerpted from
What Every Citizen Should Know About Our Planet
Used with permission.

Librarians: The book version of Wecskaop is available from
M. Arman Publishing, Fax: 386-951-1101

Expanded implications of this excerpt are also
addressed in additional PDFs in this collection:

- Thin Films - Earth's razor-thin atmosphere and seas (pdf)
  Numerics, Demographics, and a Billion Homework Questions
- Conservation planning - Why Brazil's 10% is Not Enough
- Eight Assumptions that Invite Calamity
- Climate - No Other Animals Do This
- Critique of Beyond Six Billion
- Delayed feedbacks, Limits, and Overshoot
- Thresholds, Tipping points, and Unintended consequencs
  Problematic Aspects of Geoengineering
- Carrying Capacity and Limiting Factors
- Humanity's Demographic Journey
- Ecosystem services and Ecological release
- J-curves and Exponential progressions
- 102 key Biospheric understandings

Sources and Cited References

(pending)

Anson, 2009. What Every Citizen Should Know About Our Planet. M. Arman Publishing.
Anson, 1996. Marine Biology and Ocean Science. Balaena Books.
Calhoun, 1962.
Campbell, Reece, and Mitchell, 1999. Biology.
Catton, 1982.
Christian, 1950, 1956.
Christian and Davis, 1964.
Cohen, 1995. How Many People Can The Earth Support?
Duggins, 1980.
Estes and Palmisano, 1974.
Friedman, 2008.
Gause, 1932.
IPCC, 2007.
Jenkins, 2003.
Mader, 1996
Odum, 1959.
Paine 1966; 1969.
Pimm, 2001.
Raven, et al., 1986.
Raven and Johnson, 1999.
Revelle, 1976.
Scheffer, V.B. 1951. *The rise and fall of a reindeer herd.* Scientific Monthly 73: 356-362
Soule, 1985.
Stiling, 2002.