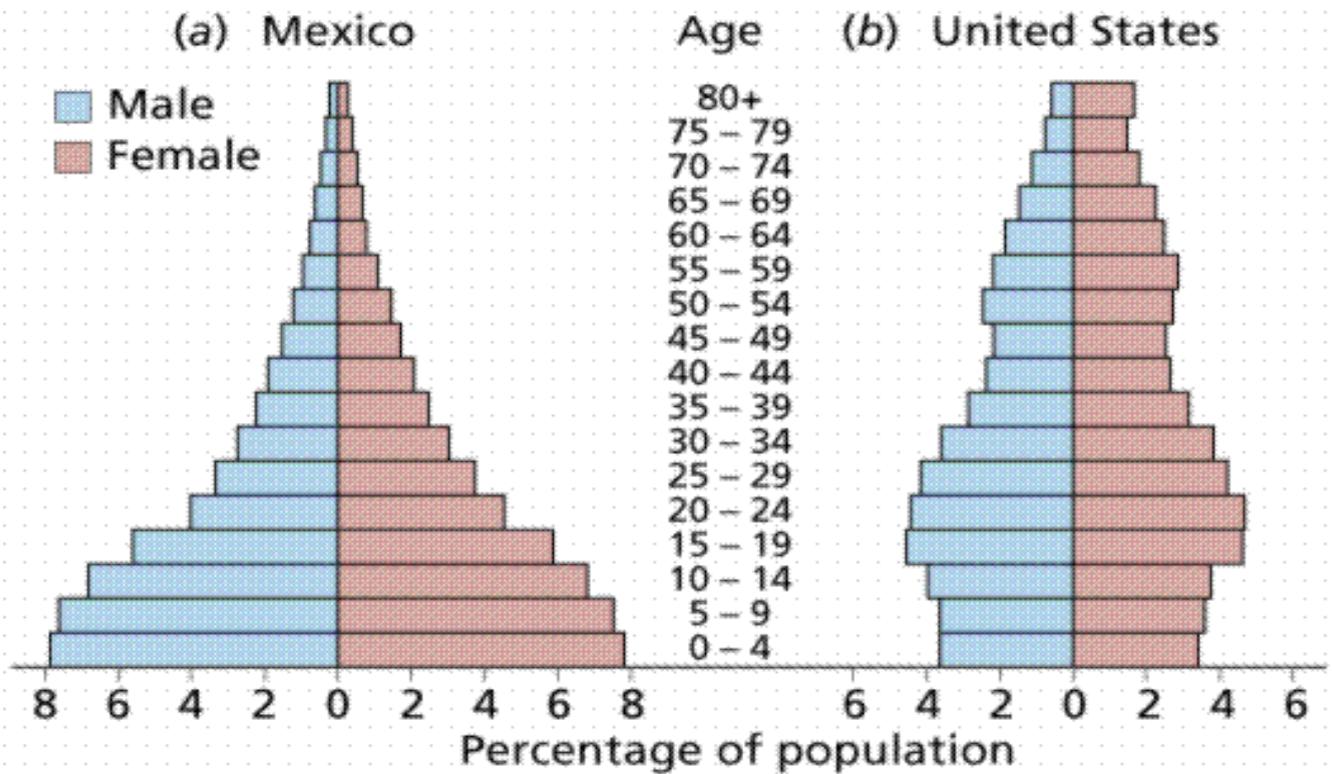


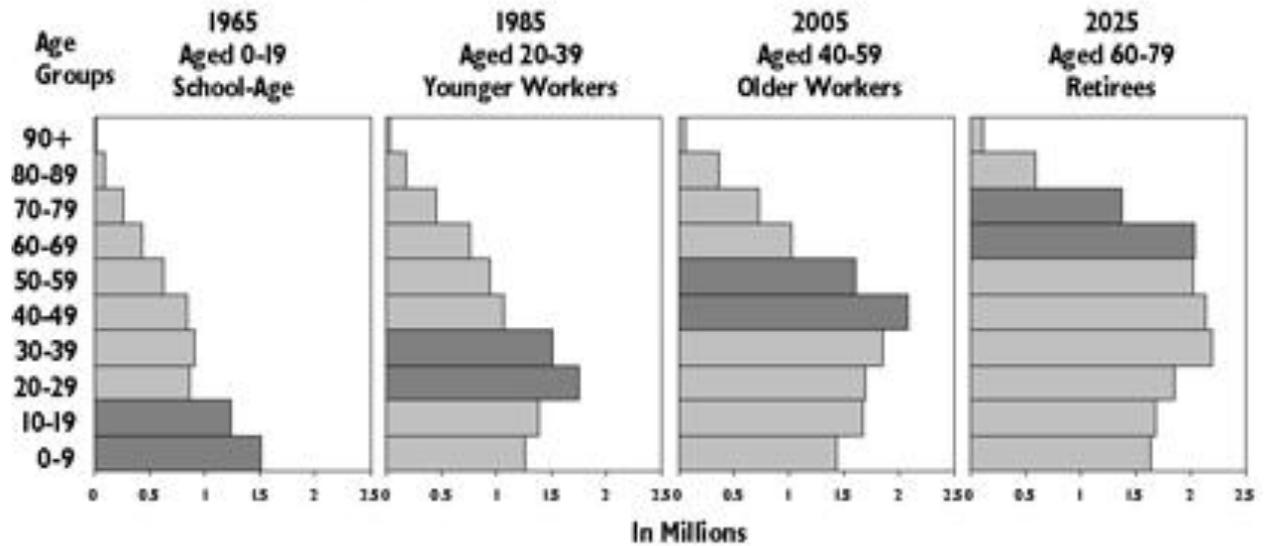
**HUMAN POPULATION BIOLOGY:** Human survivorship curves. Most modern curves are ‘Type I’ -- typical of high-parental care species (like the Dall sheep); note the vertical axis is linear, not exponential; on exponential axis, all of these would look more like the Dall sheep curve, although those for pre-modern times would be closer to a Type II curve. NOTE that, for the last several centuries, the maximum age hasn’t changed much (in fact, all the way back to Roman and Greek times, the oldest individuals lived to be around 100); what’s changed is that a larger proportion of each cohort survives to old age. The largest change is in childhood mortality (think about why...). “Life expectancy” at birth is the average age of death for a full cohort; that is much lower if 30% of a cohort dies by age 4 (e.g., the Niger curve above). The largest contributing factor in dramatic increases in life-expectancy in ‘developed’ countries is decreased childhood mortality.



Human populations have a strong ‘Type I’ – mammal-like – survivorship curve with relatively high survivorship in early years, very low mortality through adult years, and rapid decline of cohort size only in senescence. This is generally associated with high levels of parental care.

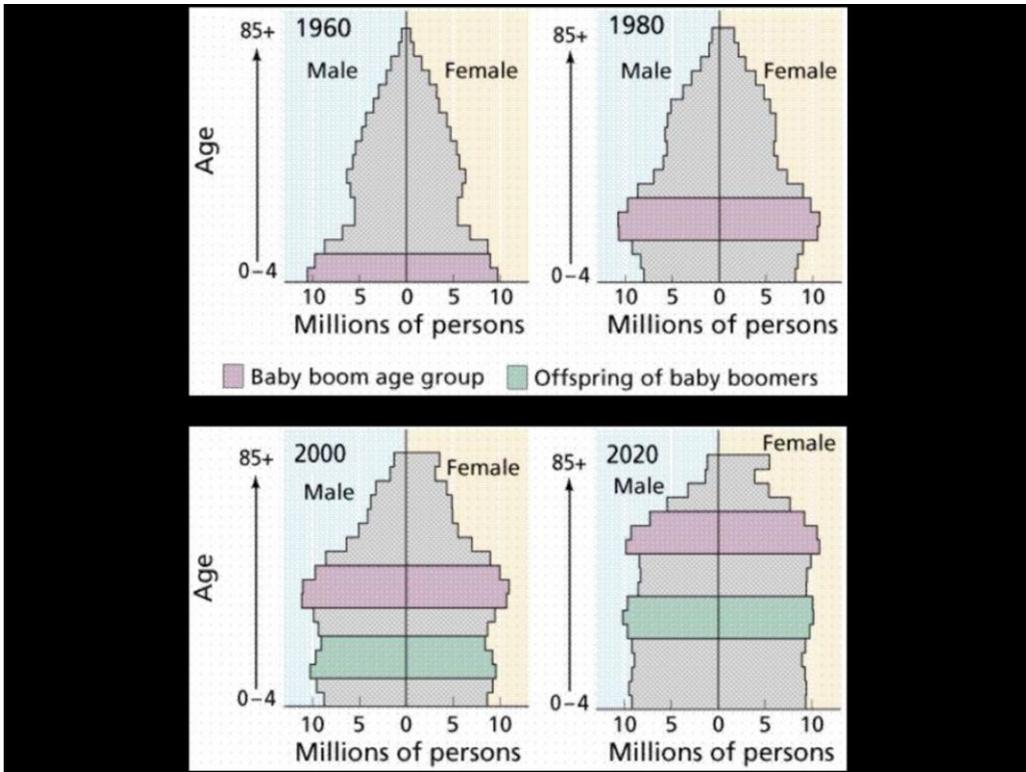
Here are some human AGE STRUCTURES for recent years; which of these AGE STRUCTURES, given similar survivorship curves of this sort (they are) can be approximately stable? (NOTE the axes for these graphs; it is standard for HUMAN DEMOGRAPHY to place age on the vertical axis).

# Baby Boomers Passing Through the Ontario Age Structure, 1965-2025

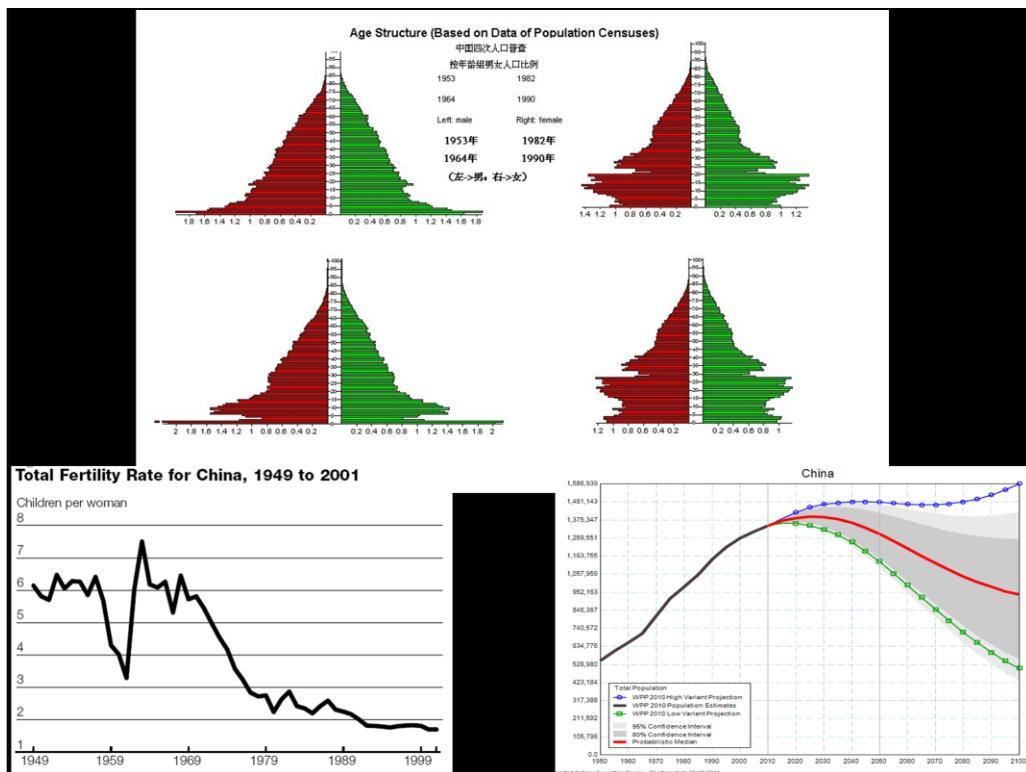


Sources: Statistics Canada, 1965 and 1985, and Ontario Ministry of Finance projections, 2005 and 2025.

Unstable age structure due to baby boom; boomers create a 'bump' moving through the age structure over time.



So does the 'baby boom echo'... (This is the United States).

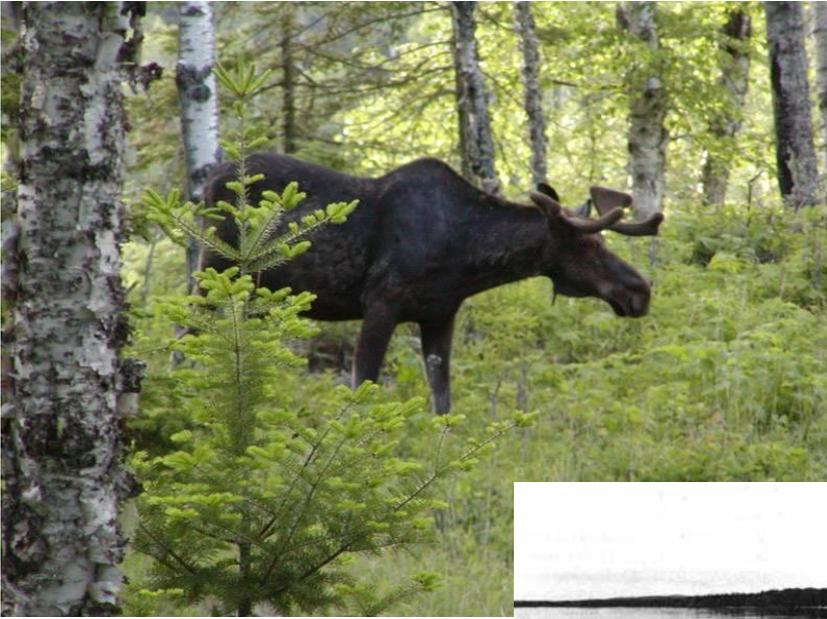


In China, catastrophic famines in the late 1950s, Mao’s ‘pro-natalist’ policies in the 1960s and early 70s, and the subsequent establishment of the 1-child policy, have produced dramatic fluctuations in cohort sizes, reflected in changing age structures (top graph). FERTILITY RATE (bottom left) is the average number of children per female over her reproductive life, and is obviously related to population birth rate). NOTE that fertility rates actually started falling BEFORE the one-child policy established in 1980. Why might this happen? There’ve also been dramatic changes in survivorship affecting age structures. Even though birth rates in recent decades are well below ‘replacement level’, population is still growing because of the very large cohorts passing through child-bearing years. However, growth rate is slowing, and China’s population is predicted to peak in about 10 years; after that it will decline, IF fertility rates remain below replacement level. Replacement level is slightly over 2; why?



In fact, populations in the wild are affected by much more complex interactions, where birth and death rates are affected by many interactions with shifting ecological factors. In particular, *interactions with other species* can be important. Populations of moose and wolves on Isle Royale, in Lake Superior, are a particularly dramatic and uniquely well-studied example (almost no other wild populations of large mammals have been studied in such intimate detail for this long); population dynamics and structures for both species have been influenced by both environmental and biological factors and feedbacks, and show very complex behaviors. Go to [www.isleroyalewolf.org](http://www.isleroyalewolf.org) for a lot of information about this study.





Moose arrived in early 20<sup>th</sup> century, presumably by swimming; they don't like to walk on ice, but they are excellent swimmers, and swimming moose have been documented at considerable distances from land. They don't have good eyesight, and probably could not see the island from the mainland, but they have excellent sense of smell.



Moose populations grew exponentially and depleted primary winter food sources (they browse on twigs and conifer needles). Photo on upper left shows a 'browse-line' on balsam fir – a tree species that is an important winter food source. All the foliage has been consumed to the maximum height that moose can reach. Smaller trees can be so heavily browsed that they are killed (upper right).

Managers at Isle Royale (not yet a national park), concerned about the degradation of habitat due to 'overpopulation' by moose, considered means of managing the moose population – of maintaining it at a more sustainable carrying capacity. They attributed the population explosion (much like what happened later with reindeer populations on the Pribilof Islands; see previous notes), in part, to lack of predators. There was an attempt, in the 1940s, to introduce wolves to the island, in the hope that death rates among moose would be increased enough to lead to population being regulated at a more moderate size. That attempt failed, largely because the wolves used had been living in captivity and/or were not successfully acclimated to the new environment



Habitat differences. Moose eat a lot of aquatic vegetation for sodium. Some trees (like deciduous birch) provide more nutritious browse. But, in the winter, moose tend to stay in 'yarding' areas under evergreen/coniferous cover because it is energetically costly for them to move through deep snow, and evergreen canopies reduce snow depth on the ground. Conifer forests, however, don't provide as much food. In deep-snow winters, the energetic cost of moving through the snow can be greater than the benefits of reaching more nutritious food, so the moose stay in the 'yards', burning stored fat and slowly starving...



Then wolves arrived on their own in the late 1950s by crossing an ice bridge from Ontario; wolf packs can travel 25-40 miles in a day, and they travel easily over snow and ice. Until recently, ice bridges formed between the mainland and Isle Royale every 3-4 years. They've become quite unusual in the last 20 years, and climate predictions suggest they're going to become a thing of the past within the next decade or two.

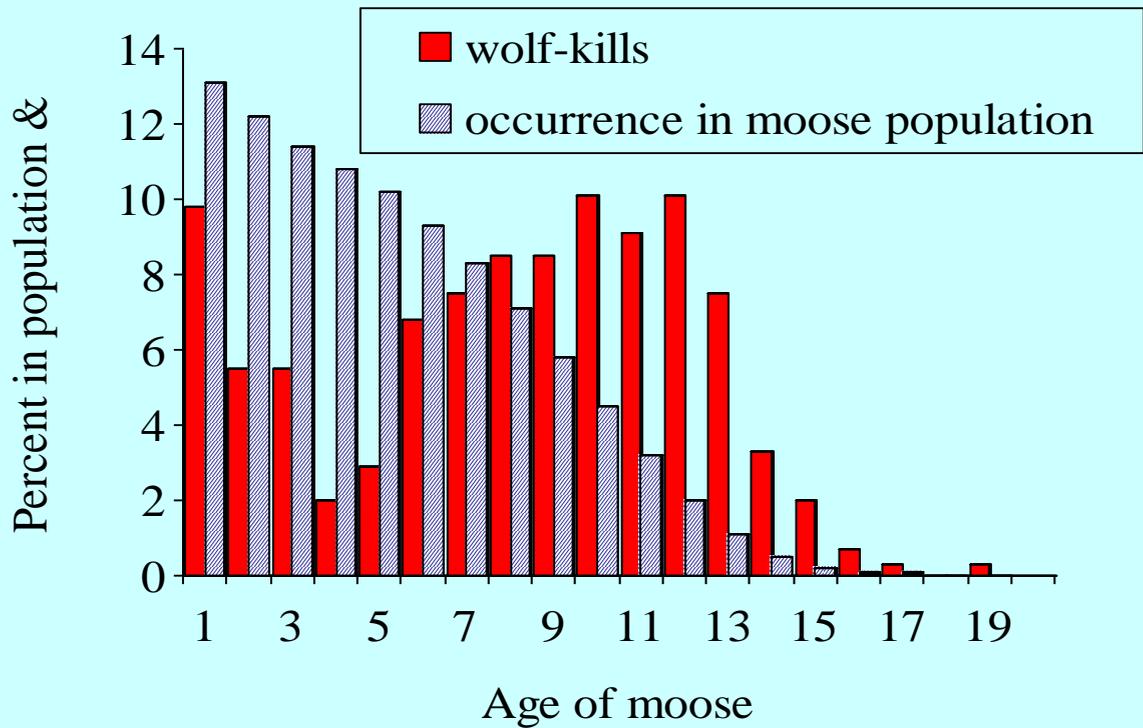


The very large and poorly nourished moose population was an easy and abundant food source for the wolves, and they started exploiting it. Note that wolves are extremely social; they generally live in packs (typically 4-6 animals, usually closely related; sometimes more) and hunt cooperatively; hunting success depends on pack dynamics, including effectiveness of leadership. Typically only one pair of wolves in a pack (the alpha male and female) reproduce, and the whole pack contributes to feeding the young.

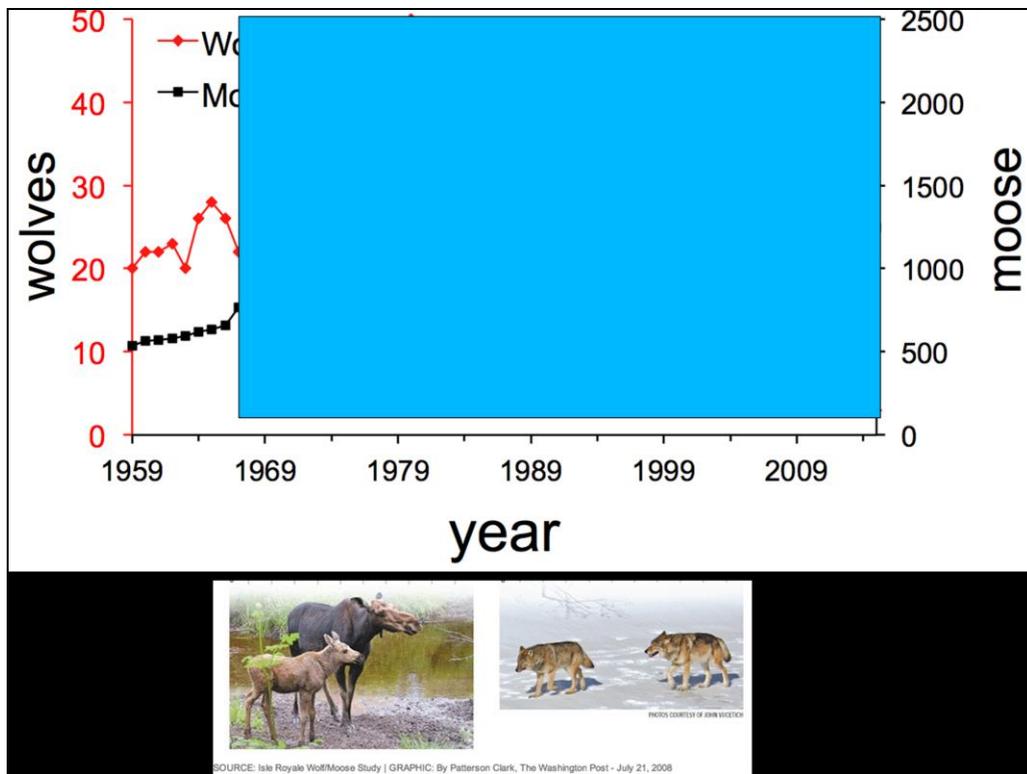


*In 1996 carcasses of 175 dead moose were examined, and skulls and other specimens accumulated at the summer research cabin on Rock Harbor.*

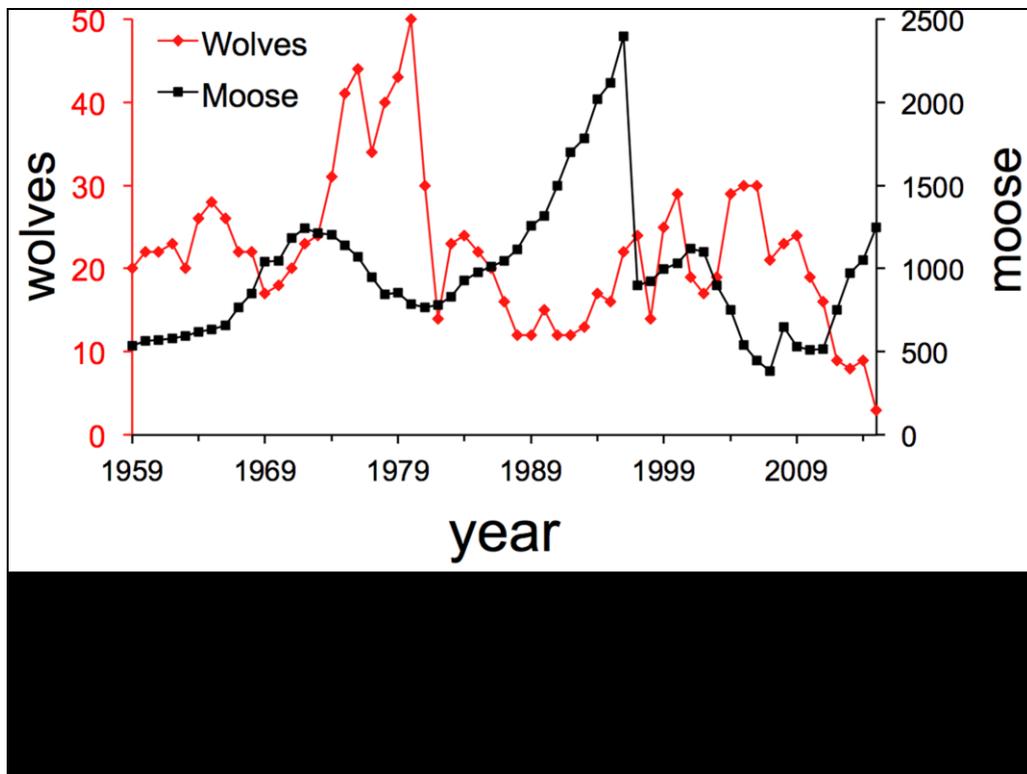
For the last 50 years, biologists from Michigan Technological University have been monitoring moose and wolf populations. Using aerial observations in the winter, they track moose-kills by wolves (and other mortality). Later, they visit kill sites and use skeletal remains to reconstruct age and condition of the moose killed by wolves. Individual wolves can be recognized by color and appearance; some were tranquilized and radio-tagged. These long-term studies provide a nearly unique perspective of population dynamics in a large animal predator-prey system. This cabin is their permanent ‘field lab’ on Isle Royale, with a collection of skulls and other skeletal remains. Check out <http://www.isleroyalewolf.org/wolfhome/home.html>



Many interesting patterns emerged. For example, not all moose are equally vulnerable to wolves; they prey disproportionately on young and old moose. The top graph shows an *age-structure* for the moose population (blue-hatched bars), and a *death assemblage* for moose killed by wolves (red bars). Healthy young adult moose (ages 3-5) are essentially immune to predation; in fact, they can seriously injure or even kill wolves, and wolves can quickly sense, by its behavior, whether a moose is vulnerable. The lower right chart shows patterns of wolf ‘testing’ and attack...



Conventional ecological theory at the time held that predator-prey systems would reach a kind of equilibrium. During the first years of the study, this seemed like it might be the case; moose population on the island had dropped to N of about 500 (black line and right-hand vertical axis), and the wolf population stabilized at about 24 (red line, left vertical axis) animals organized into, usually 1 or 2 large packs (packs maintained exclusive territories, conducting ‘border wars’ to defend against neighboring packs).



But, over the longer term, things got really complicated! Both populations showed dramatic changes, and it is difficult to see anything resembling stability or equilibrium for more than a few years (unfortunately, most ecological studies don't last more than a few years!). CAUSES for many of these changes are reasonably well understood, and range from changes in physical environment (winter weather) and biological environment (changes in forest composition), to parasites and diseases, to changes in the social structures of the wolf population. For instance, the large increase in wolf population in the 1970s (to a maximum of nearly 50) probably involved both response to increasing moose population (maybe due to mild winters), AND loss of a dominant alpha pair in a large pack leading to 'splintering' of the wolf population into 4 packs – and therefore a much higher birth rate (remember that only one pair breeds in each pack). The crash in the wolf population in 1980 was due to the accidental introduction of a disease – canine distemper – from a dog visiting the park with its owner (illegally; dogs are not permitted officially...); this was probably a large factor in the exponential growth of moose population in the 1980s and 90s.

Wolves don't always hunt 'efficiently'; sometimes they kill lots more than they eat. (graphic didn't translate well; but When times are good (about 25% of the time), wolves get 2-4 times more food per capita than when times are bad (another 25% of the time). Maximum kill rate is 2-1/2 times the average kill rate. Minimum kill rate is 15% of typical kill rate.



This may have a lot to do with weather; deep-snow winters weaken moose to the point where they are



So climate interacts with moose vulnerability interacts with kill success interacts with pack size interacts with kill rate...

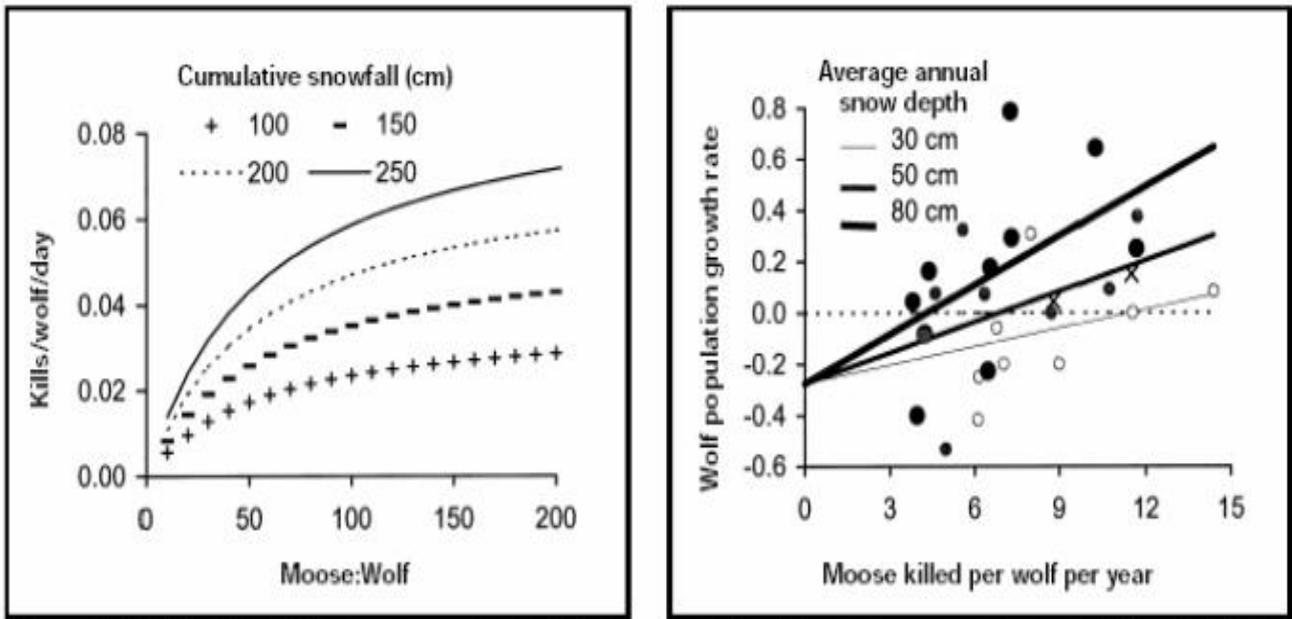


Figure 10. (Left) Wolves kill more moose (y-axis) during years when there are more moose per wolf (x-axis). These relationships, called functional response and numerical response, together determine the nature of predator-prey dynamics. Winter climate has an important impact on both relationships. In years with more snow, wolves not only kill more moose (left), they are also more efficient at converting moose killed into wolf population growth (right), possibly because moose are less fit.

These graphs show the relationships between snowfall, ratio of moose to wolves, kill rate, and rate of wolf population growth.

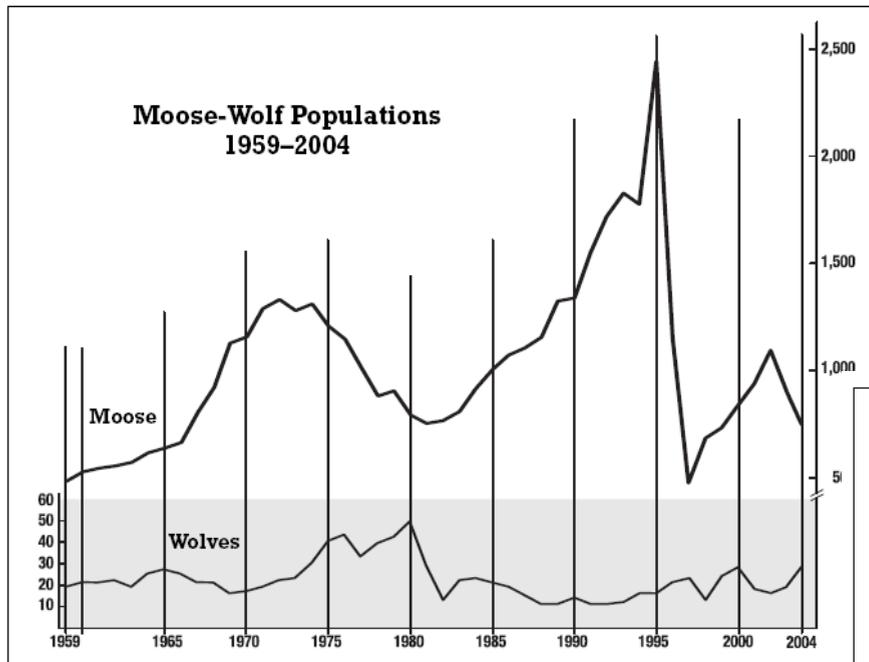


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2004. Moose population estimates during 1959-1993 based on population reconstruction from recoveries of dead moose, whereas estimates from 1994-2004 were based on aerial sur

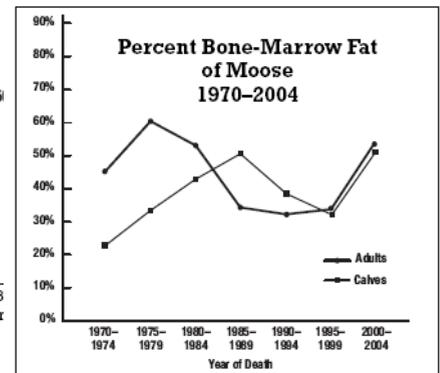
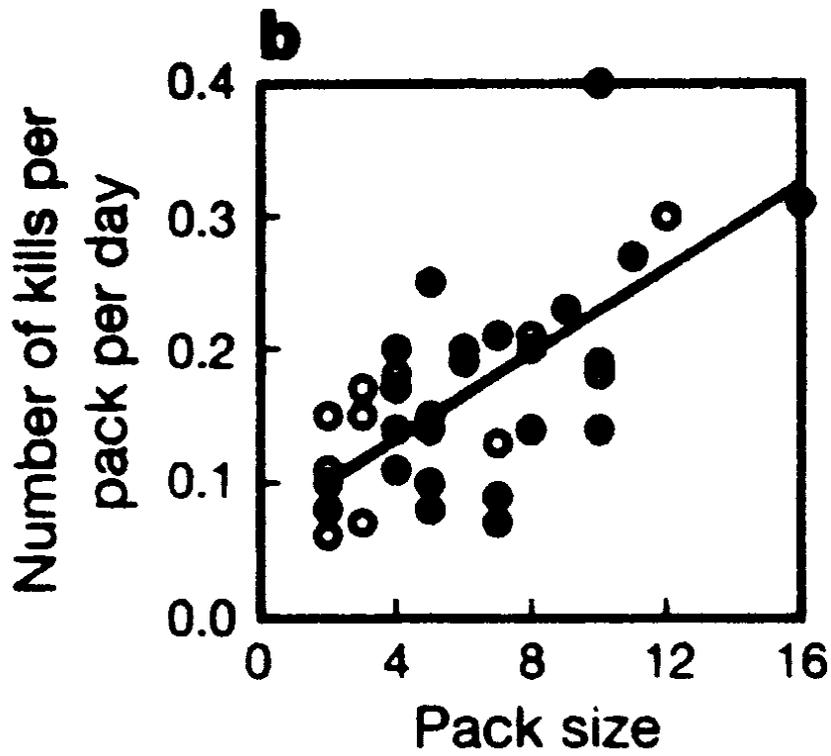
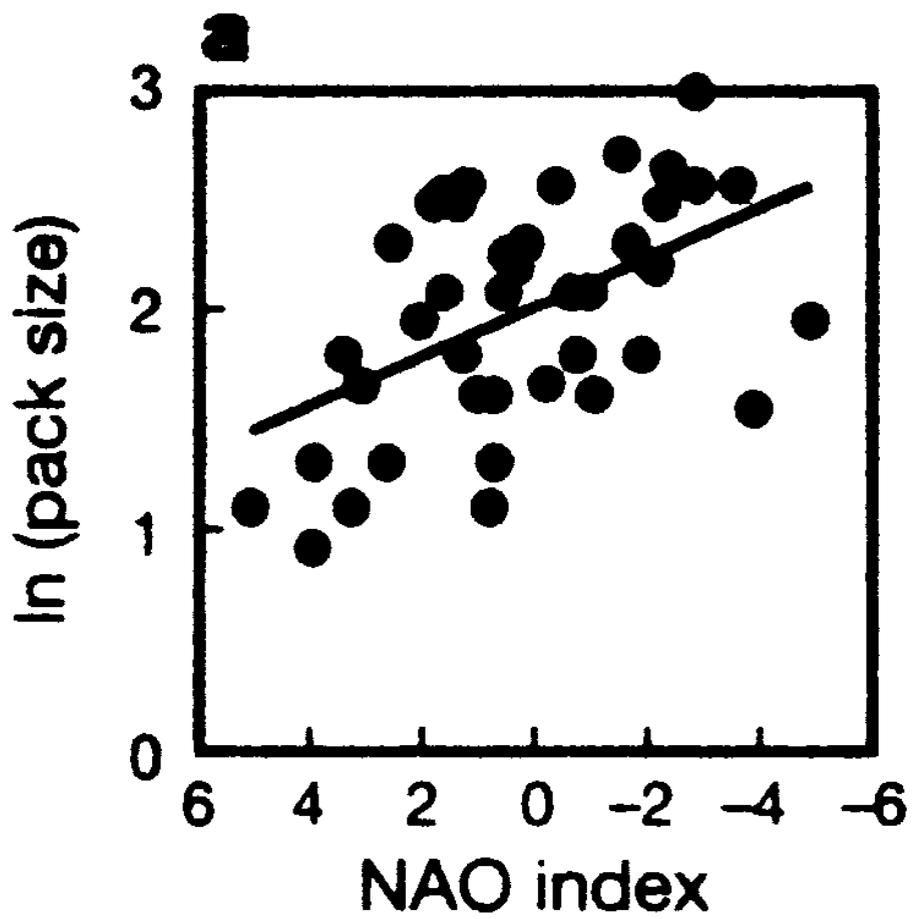


Figure 17. Long-term trends in moose bone-marrow fat. Data for calves (which best reflect current conditions) represent mean levels, whereas data for adults is the proportion with greater than 70 percent marrow fat. Over the past five years, marrow fat levels have been relatively high.

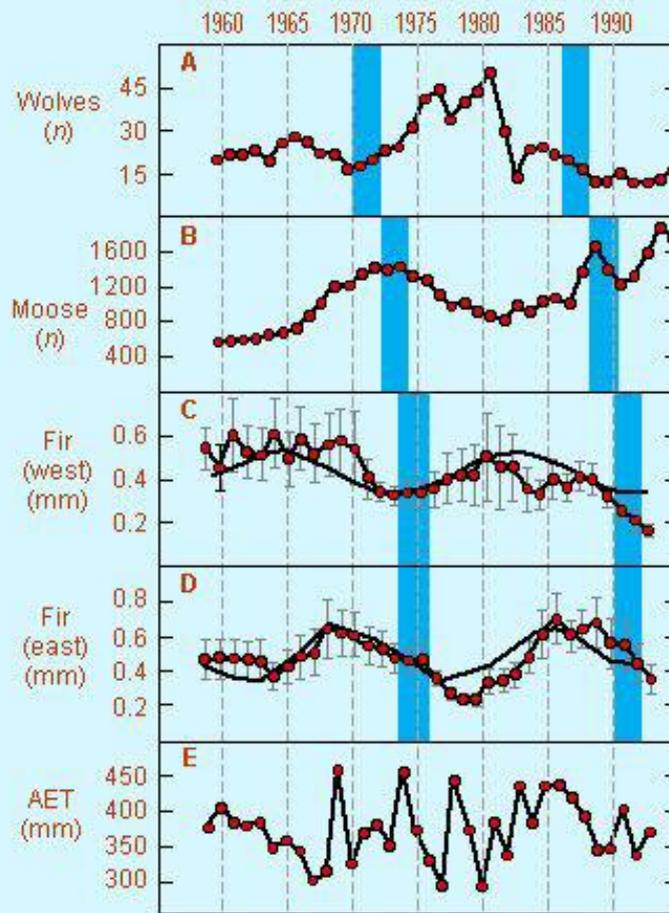
Nutritional status of moose populations can be assessed by measuring bone-marrow fat levels in moose carcasses. Higher moose populations correspond to lower fat levels, suggesting competition for food – *density-dependent processes* – affecting moose populations (perhaps mediated through predation).



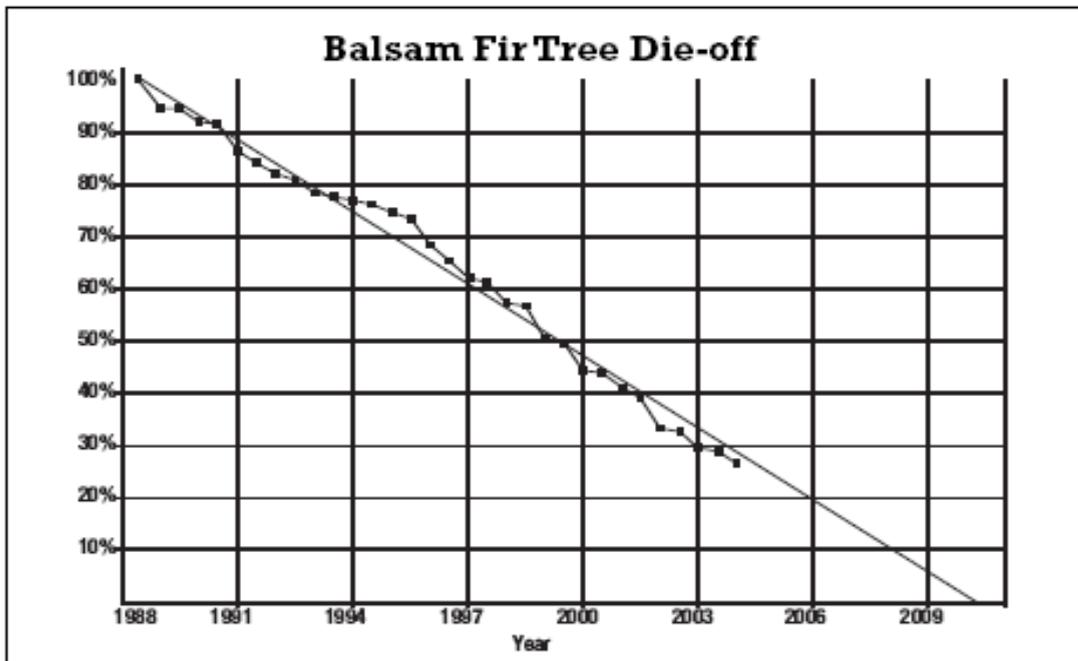
Kill rate per pack (and per individual wolf) increases with wolf pack size. The “NAO” – North Atlantic Oscillation – is a climatic cycle.



07 illustrated that vulnerable prey were not readily located by wolves  
In years when moose were healthier, wolves consumed each kill more fully.

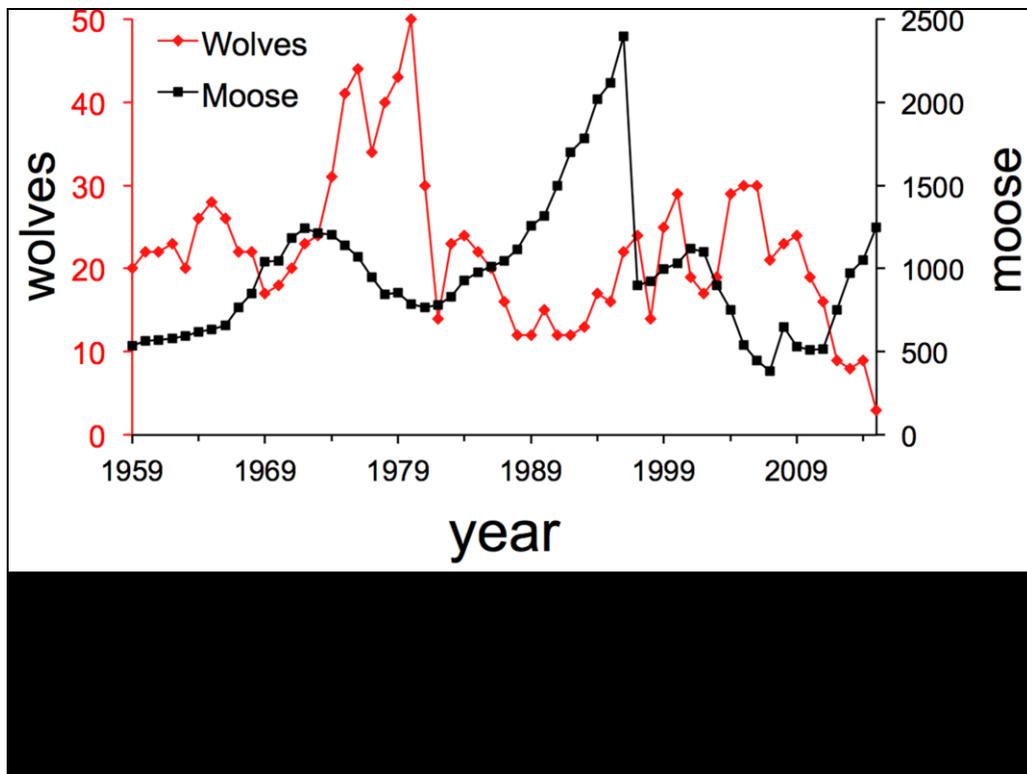


The focus on wolf predation is driven, in part, by a presumption that moose populations are regulated by predation – by the effects of a higher trophic level (more on this later) – often called ‘top-down’ regulation. Some data suggest climate differences regulate plant productivity – moose food availability – thus driving moose populations from the ‘bottom up’. On the other hand, when wolves depress moose populations, plant populations may respond by increased growth– t ‘top-down’ influence propagating down the food chain. “Fir” curves show measured growth rates (ring-widths) for fir trees in two areas. Note that “AET” is actual evapotranspiration - related to rate at which trees pump water through foliage -- but don’t worry about that too much.



**Figure 19.** Balsam fir trees in the forest canopy that were tagged in 1988 have steadily died off without replacement. The remainder are expected to die by 2009-2010, and at that point a seed source for this species will be absent over 75 percent of Isle Royale. The demise of this species is ultimately caused by moose herbivory.

And food availability for moose may simply be changing due to long-term change in abundance of fir trees as they are competitively displaced by other species.



Following the distemper-caused crash in wolf populations, biologists began to note symptoms of inbreeding (high rates of skeletal malformation, early and severe arthritis, etc) in the wolf populations, and concerns were raised about the resulting fate of the population. Some suggested introducing new wolves from the mainland to reintroduce genetic diversity, but this was opposed by many as unwarranted human intrusion (and, in fact, it went against national park standard regs). Then the wolf population showed a substantial recovery. It wasn't clear at the time, but this appears to be due to a single male wolf introducing itself (by crossing the ice again) about 1997. This male became the alpha male in the main pack at that time, and fathered many offspring with two successive alpha females. His offspring then became alpha members of other packs (there were up to 4 for a while). A decade after his arrival, nearly ALL of the wolves on the island were his descendants, and there were multiple instances of alpha pairs being half siblings or parent-child. This is *extreme* inbreeding.

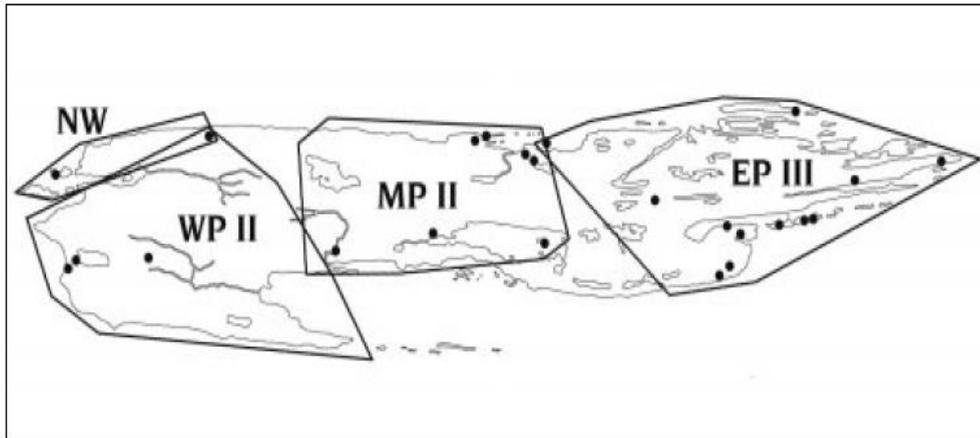


Figure 2. Wolf pack movements and moose carcasses (wolf-kills and otherwise) during the 1997 winter study. All packs except NW actively marked their territory.

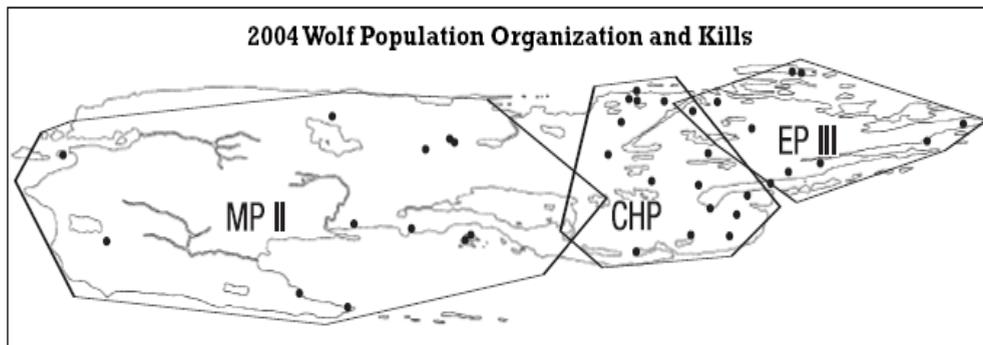
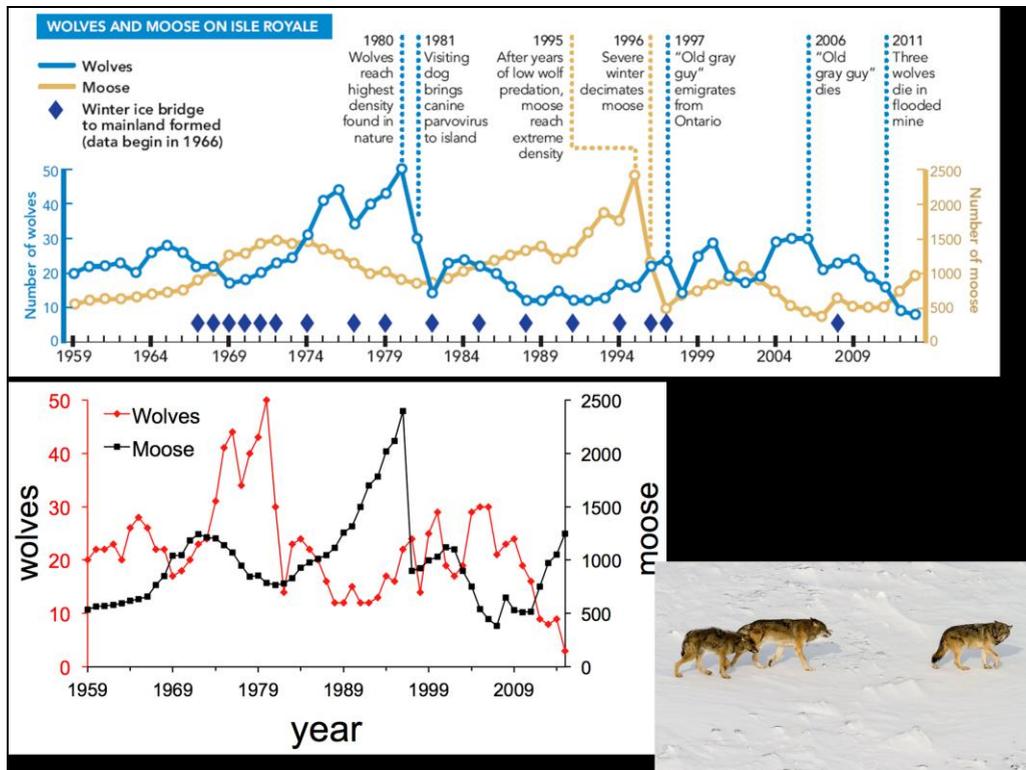


Figure 5. Wolf pack movements and moose carcasses (almost all fresh wolf-kills) during the winter study in 2004. Scent-marking was observed by all three of the packs.

Wolf pack interactions have varied greatly, with more packs, there can be more wolves – but packs fight for territory. Some packs are better hunters than others. Some years kills are concentrated along shore (where ‘yarding’ areas allow moose to overwinter in less deep snow); other years more widely scattered...



The wolf population has now crashed again – probably due in large part to inbreeding. Ice bridges have not occurred since the ‘old gray guy’s arrival, so there’s been no opportunity for further ‘genetic rescue’. An accidental drowning of three wolves in 2011 severely aggravated the situation. There only three wolves on the island in 2015; a breeding pair and their yearling offspring. The offspring (in rear of the photo) shows severe malformation and appears unhealthy in general. Expectations are that these last wolves will not survive long, and the wolf population will die out after about 65 years on the island. MEANWHILE, moose populations have been maintained at relatively low levels by changes in forest composition (and food source), very heavy infestations of winter ticks (due to milder winters?).