What scale of human impact on large carnivores is compatible with restoring ecosystem function?

Dr. Brad Bergstrom, Department of Biology, Valdosta State University, Valdosta, GA 31698





Human-caused mortality in mammalian carnivores

Premise:

1) Extinction, Extirpation, Range Contraction and Population Reduction have removed (Ecologically Effective densities of) large carnivores (= apex predators) from ecosystems;

2) Now fragmented, isolated populations further reduced by Harvest, Control Kills, Poaching, and Roadkill;

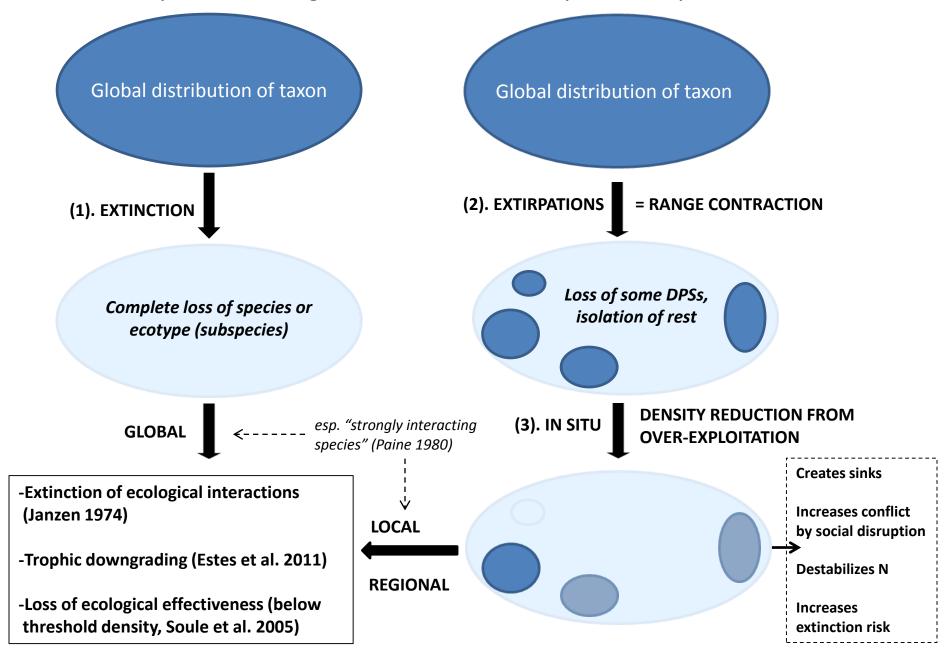
3) Human-caused mortality is largely Additive, not Compensatory (= replaceable), may not be offset by increased Recruitment, and can even be Super-Additive, due to Breeder Loss, Infanticide, Pack Dissolution, etc.;

4) Loss of Apex Predators disrupts Trophic Cascades: a) increases prey irruptions and overbrowsing; b) destabilizes plant communities, soils, and nutrient flows; c) increases invasions and disease; d) destabilizes ecosystems and reduces biodiversity (Keystone effect);

5) Sure, let's argue about "sustainable" mortality, but "sustainable" with depressed density isn't good enough to restore #4 ("Bristol Bay Fallacy");

6) Ecosystem function of apex predators not fully restored without natural, intrinsically regulated social structure.

Hierarchy of loss of large-carnivore biodiversity and ecosystem services



Recent Terrestrial Mammalian Predator Extinctions

Cape lion (Panthera leo melanochaitus) – 1858 Falkland Islands wolf (Dusicyon australis) – 1867 Sea mink (Neovison macrodon, NE North American coast) – 1860s Cape serval (Leptailurus serval serval, South Africa) - ? Atlas bear (Ursus arctos crowtheri) - 1870s Hokkaido wolf (Canis lupus hattai) – 1889 Honshū wolf (Canis lupus hodophilax) - 1905 Sardinian lynx (Lynx lynx sardiniae) - 1908 Bernard's wolf (Canis lupus bernardi, Banks and Victoria islands, Canada) - 1920 Thylacine (Thylacinus cynocephalus, Tasmania) – 1936 Eastern cougar (Puma concolor couquar, Eastern US) - 1930s Cascade mountains wolf (Canis lupus fuscus) - 1940 Bali tiger (Panthera tigris balica) - 1940s Barbary lion (Panthera leo leo) – 1950s Mexican grizzly bear (Ursus arctos nelsoni) - 1960s Caspian tiger (Panthera tigris virgata) 1970s, Tajikistan Javan tiger (Panthera tigris sondaica) - 1976 Japanese river otter (Lutra lutra whiteleyi) – 1979 Formosan clouded leopard (Neofelis nebulosa brachyura) – 1983

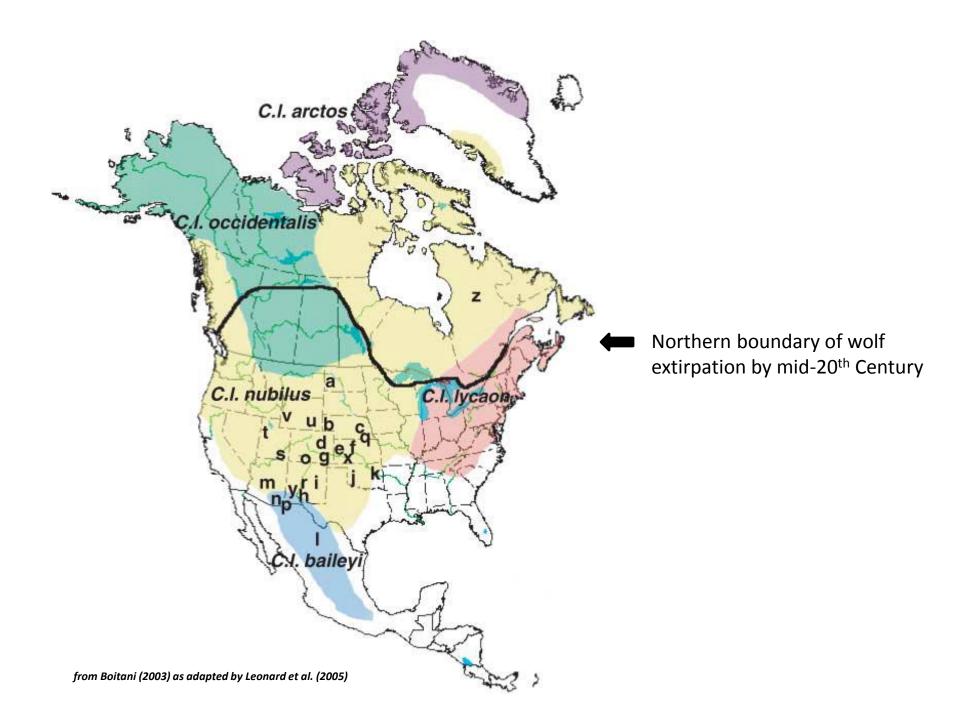
Late Pleistocene "overkill" drove many North American large carnivores extinct 10,000 - 12,000 years ago, because ...

- " ... the large mammalian herbivores of the North American Pleistocene were primarily predator limited and at low densities, and therefore highly susceptible to extinction when humans were added to the predator guild." (Ripple and van Valkenburgh 2010).
- "Overkill" victims included canids (*Canis dirus*), felids (*Panthera leo atrox*, *Homotherium serum, Smilodon fatalis, Miracinonyx* spp.), and ursids (*Arctodus simus, Tremarctos floridanus*).









North American Wolf Extirpation Dates

New England – 1840

Smoky Mtns – 1890 Adirondacks – 1900



Western US - 1930

Red Wolf, east of Miss. Riv. – 1944 kil Red Wolf species (TX/LA) - 1975

100,000 wolves/year killed from 1870-77

pbs.org

Mexican Gray Wolf (in Mexico) - 1977

Species	Area of contraction	Area of expansion	Area of persistence	Area of net loss (–) or increase (+)
Contractions of more than	20%			
Black-footed ferret	100	0	0	-100
Elk	77	3	23	-74
Pronghorn	64	0	36	-64
Swift fox	68	8	32	-60
Dall's sheep	64	10	36	-54
Grizzly bear	55	2	45	-53
Fisher	50	3	50	-47
Gray wolf	42	0	58	-42
Lynx	40	1	60	-39
Black bear	41	2	59	-39
Wolverine	39	2	61	-37
Cougar	40	4	60	-36
Musk ox	35	4	65	-31
Mountain goat	43	12	57	-31
River otter	25	0	75	-25
Bighorn sheep	40	15	60	-25
Caribou	24	0	76	-24
Marten	21	2	79	-19

Table 2. Percentage contraction, expansion, persistence, and net loss or increase of areas for 43 North American carnivores and ungulates.

11 spp. of native North American carnivores have experienced historic range contractions of > 20%; 5 large carnivores have shown range contractions of 36-53% continent-wide (Laliberte and Ripple 2004).

The hidden biodiversity crisis: loss and depletion of populations

- Less than one-fifth of Earth's land surface still harbors the same large-mammal fauna as it did in 1500 (Morrison et al. 2007).
- One percent of *all populations* of plant and animal species go extinct every year (Bamford et al. 2003, *Trends Ecol Evol*), which equals 15-35% of all populations in a human generation; this represents a loss of geographic and genetic diversity and cultural memory (e.g. ancestral feeding or breeding grounds, or migration routes).

The US Endangered Species Act (ESA, 1973) aims to prevent extirpation across a "significant portion of [a species'] range" and also of DPSs, which may be evolutionarily or ecologically distinct units of a species, and certainly are integral components of local/regional ecosystems. How well does ESA work? **Fig. 1. Worldwide population estimates of large-carnivore species.** Error bars represent the low and high range of the estimates when available. Population estimates were not available for all species. Species ranges vary widely, and range sizes can have a strong influence on species population levels (table S1). Sources: Gray wolf (*90*), all other species IUCN (*91*).

Ripple et al. (2014 Science 343, 1241484)

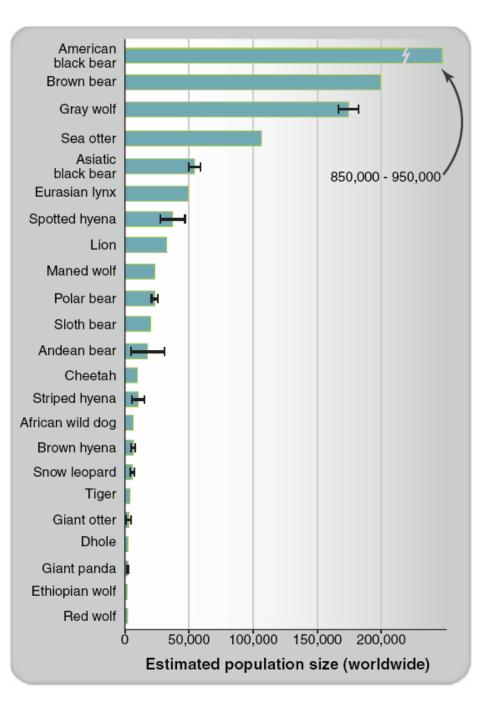


Table 1. Large-carnivore species list, body mass (in kilograms), diet, endangerment status, population trend, and percent of historical range occupied. Body masses are from Gittleman (*15*), Mammalian Species Accounts, and the Animal Diversity Web. Diet categories are from

Hunter (1) as follows: M, meat eater; V, vegetation and/or fruit eater; O, omnivore. Species status and trend are from the IUCN Red List (16): LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered.

Family/species*	Common name	Mass, diet	IUCN status (trend)	% of historical range	Reference for % of historical range
Canidae					
Canis lupus	Gray wolf	33, M	LC (stable)	67	(1)
Canis rufus	Red wolf	25, M	CR (increasing)	<1	(91)
Chrysocyon brachyurus	Maned wolf	23, 0	NT (unknown)	68	(2)
Lycaon pictus	African wild dog	22, M	EN (decreasing)	10	(17)
Cuon alpinus	Dhole	16, M	EN (decreasing)	-	_
Canis dingo†	Dingo	15, M	VU (decreasing)	84	(20)
Canis simensis	Ethiopian wolf	15, M	EN (decreasing)	2	(17)
Felidae					
Panthera tigris	Tiger	161, M	EN (decreasing)	18	(3)
Panthera leo	Lion	156, M	VU (decreasing)	17	(17)
Panthera onca	Jaguar	87, M	NT (decreasing)	57	(3)
Acinonyx jubatus	Cheetah	59, M	VU (decreasing)	17	(17)
Panthera pardus	Leopard	53, M	NT (decreasing)	65	(3)
Puma concolor	Puma	52, M	LC (decreasing)	73	(3)
Panthera uncia	Snow leopard	33, M	EN (decreasing)	-	-
Neofelis nebulosa	Clouded leopard	20, M	VU (decreasing)	-	_
Neofelis diardi	Sunda clouded leopard	20, M	VU (decreasing)	_	_
Lynx lynx	Eurasian lynx	18, M	LC (stable)	-	-
Mustelidae					
Enhydra lutris	Sea otter	28, M	EN (decreasing)	-	-
Pteronura brasilliensis	Giant otter	24, M	EN (decreasing)	-	-
Aonyx capensis	Cape clawless otter	19, M	LC (stable)	-	-
Ursidae					
Ursus maritimus	Polar bear	365, M	VU (decreasing)	_	-
Ursus arctus	Brown bear	299, 0	LC (stable)	68	(3)
Ailuropoda melanoleuca	Giant panda	134, V	EN (decreasing)	_	-
Ursus americanus	American black bear	111, 0	LC (increasing)	59	(35)
Tremarctos ornatus	Andean black bear	105, 0	VU (decreasing)	-	-
Ursus thibetanus	Asiatic black bear	104, O	VU (decreasing)	-	-
Melursus ursinus	Sloth bear	102, 0	VU (decreasing)	-	-
Helarctos malayanus	Sun bear	46, O	VU (decreasing)	-	_
Hyaenidae					
Crocuta crocuta	Spotted hyena	52, M	LC (decreasing)	73	(17)
Hyaena brunnea	Brown hyena	43, 0	NT (decreasing)	62	(17)

from Ripple et al. (2014, Science 343, 1241484)

Attitudes, perspectives, and science...

POLICY OF THE U. S. BIOLOGICAL SURVEY IN REGARD TO PREDATORY MAMMAL CONTROL

"The fact remains that the bureau must work for the *eradication* of certain species locally where their destructiveness is so impressive that *no other policy of handling them is permissible*. For example, the *gray wolf* and the *prairie dog* are so deleterious to agriculture and stock raising that *their presence in some localities can not be tolerated*. Other species, such as the *coyote* and the *ground squirrel*, are so prolific and occur over such wide areas that *their extermination, even if desired*, *would be impossible*. The Bureau of Biological Survey is *not* embarked upon a *general extermination program*, and the main objective is so to control the predatory animals and rodent pests as to reduce economic losses to a minimum."

Paul G. ReddingtonBureau of Biological Survey,U. S. Department of Agriculture,Washington, D. C.April 4, 1929

Published in Journal of Mammalogy 10(3):276-279.

Cultural and legal devaluation of mammalian predators

- Don Peay, founder of Sportsmen for Fish and Wildlife, says wolves are multiplying exponentially, putting wildlife and people at risk. "Wolves will destroy their food supply, and they'll kill people. That's why our pioneers got rid of wolves in the first place. Wolves are way out of control in the west, and it's time for Congress to step in and reduce wolf populations before they kill people," he says.

Hunters say they've spent a fortune on programs to build up big-game herds; now wolves are wiping them out. "They're destroying our wildlife herds right now John. They destroyed Yellowstone, they're destroying the moose population around Jackson," Peay says.

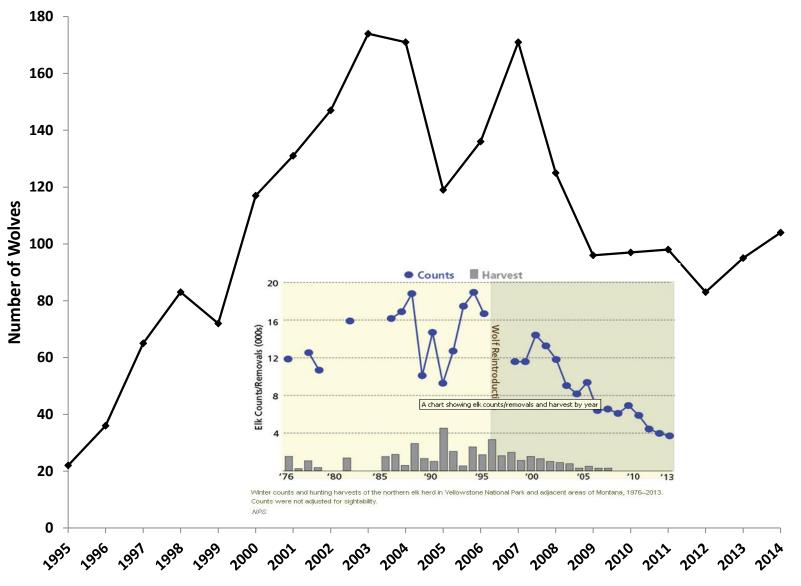
KSL News Radio (KSL.com) Salt Lake City, UT March 14, 2010

Definition of "Predator"

- Under many states' wildlife laws, deer, elk, bighorn sheep, cougars and black bear are classified as "big game" (but no bag limit on cougars in Texas); several other carnivores (and a few rodents) are classified as "furbearers." But many states legally designate certain native wildlife as "<u>predator</u> " (synonymous with varmint), and they can be killed without license or restriction. In Wyoming, this applies to coyote, jackrabbit, porcupine, raccoon, red fox, skunk and stray cat; and in their short-lived state-management period, it applied to gray wolves over 80% of the state.

Current laws on the books approving bounties on predators: coyotes (6 states), bobcats (2), wolves (3). Only 13 states legally prohibit wildlife bounties.

Wolf population of Yellowstone National Park since reintroduction



A THE R. L. P. M. LANSING

AN ESKIMO LEGEND

"In the beginning there was a Woman and a Man, and nothing else walked or swam or flew in the world until one day the Woman dug a great hole in the ground and began fishing in it. One by one she pulled out all the animals, and the last one she pulled out of the hole was the caribou. Then Kaila, who is the God of the Sky, told the woman the caribou was the greatest gift of all, for the caribou would be the sustenance of man. "

"The Woman set the caribou free and ordered it to go out over the land and multiply, and the caribou did as the Woman said; and in time the land was filled with caribou, so the sons of the Woman hunted well, and they were fed and clothed and had good skin tents to live in, all from the caribou."

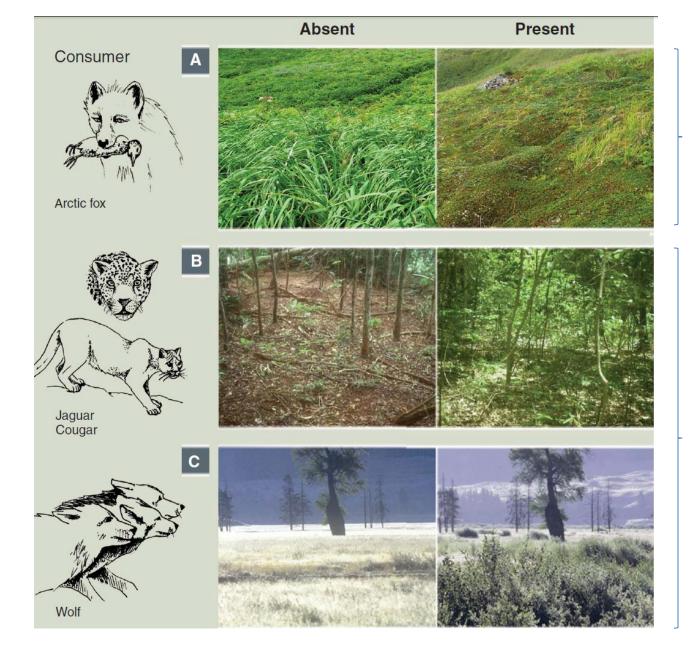
"The sons of the Woman hunted only the big, fat caribou, for they had no wish to kill the weak and the small and the sick, since these were no good to eat nor were their skins much good. And, after a time, it happened that the sick and the weak came to outnumber the fat and the strong, and when the sons saw this they were dismayed and they complained to the Woman."

"Then the Woman made magic and spoke to Kaila and said: 'Your work is no good, for the caribou grow weak and sick, and if we eat them we must grow weak and sick also.' "

"Kaila heard, and he said 'My work is good. I shall tell Amorak [the spirit of the Wolf], and he shall tell his children, and they will eat the sick and the weak and the small caribou, so that the land will be left for the fat and the good ones."

"And this is what happened, and this is why the caribou and the wolf are one; for the caribou feeds the wolf, but it is the wolf who keeps the caribou strong."

As retold by Farley Mowat in *Never Cry Wolf*



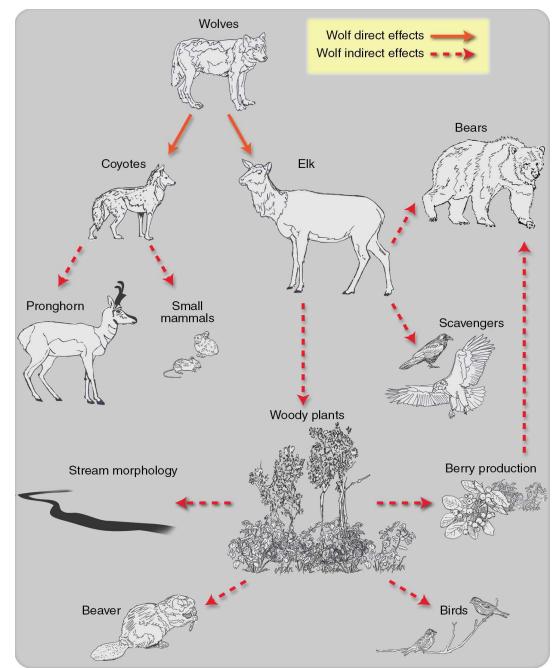
Invasive Predator: negative indirect ecosystem effects

Native Predators: positive indirect ecosystem effects

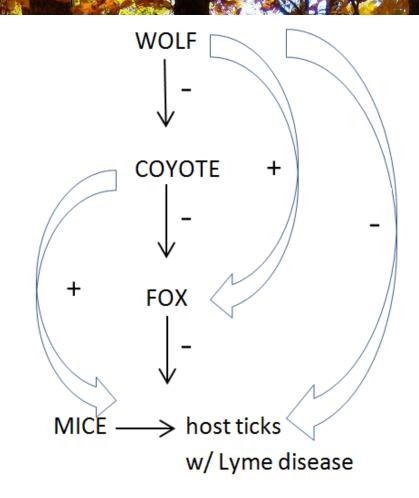
from Estes et al. (2011, Science)

Fig. 4. Conceptual diagram showing direct (solid lines) and indirect (dashed lines) effects of gray wolf reintroduction into the Greater Yellowstone ecosystem. Wolf direct effects have been documented for elk (96) and coyotes (97), whereas indirect effects have been shown for pronghorn (98), small mammals (99), woody plants (100), stream morphology (54), beaver (55), birds (101), berry production (63), scavengers (53), and bears (56, 63). This is a simplified diagram, and not all species and trophic interactions are shown. For example, the diagram does not address any potential topdown effects of pumas, bears, and golden eagles (Aquila chrysaetos), which are all part of the Yellowstone predator guild where juvenile or adult elk are prey.

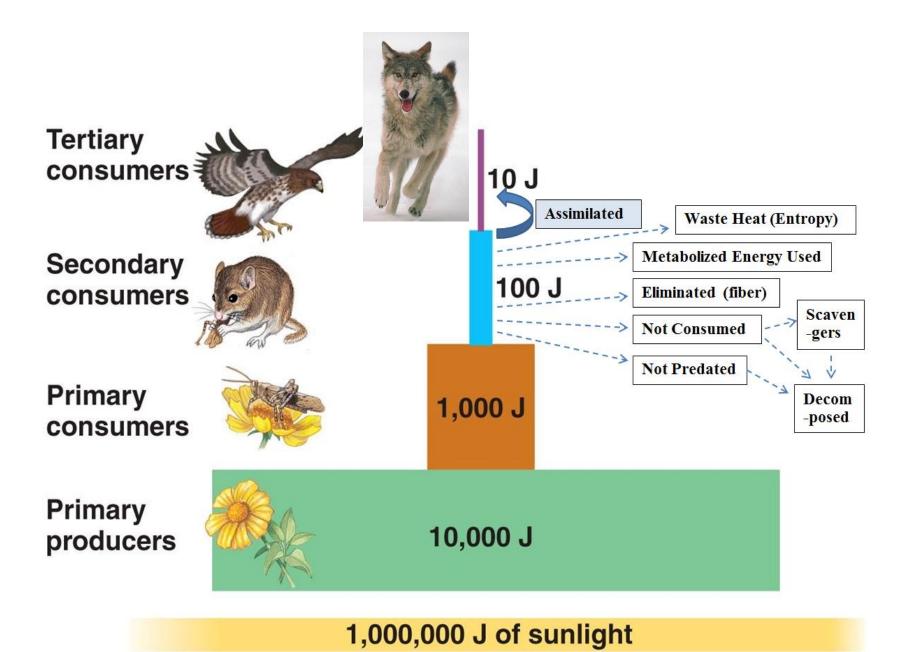
Ripple et al. (2014 Science 343, 1241484)



Top-down forcing by apex predators may mitigate human diseases



representative of Levi and Wilmers (2012)



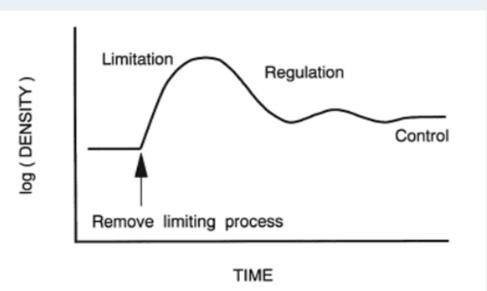
Copyright @ 2008 Pearson Education, Inc., publishing as Pearson Benjamin Cummings.

However, Primary Consumers are less abundant than Trophic Pyramid model ("Bottom-Up") predicts because they are limited by their Predators ("Top-Down)

- So said HSS (1960) in the "Earth is Green" Hypothesis. (Fretwell [1977], Oksanen et al. [1981] said this works in 3- and 5-level Food Chains.)
- Within an Intact Food Web:
 - Producers and Predators are Resource-limited and therefore compete
 BOTTOM-UP
 - Herbivores are normally Predator-limited (not plant-limited)

TOP-DOWN

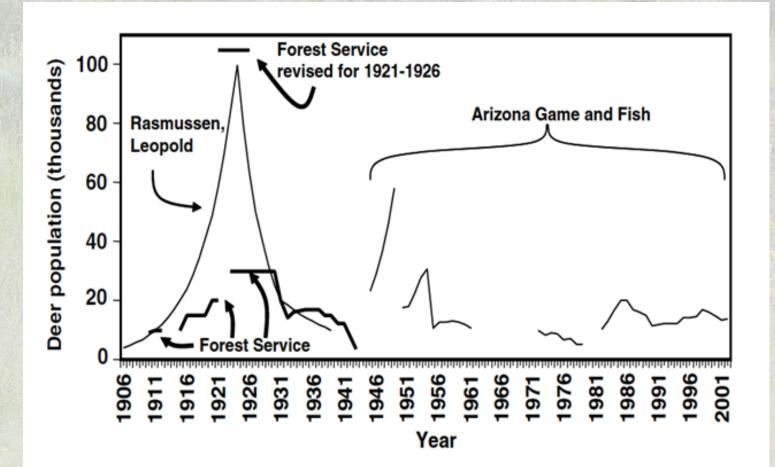
Evidence of Top-down Control (following Predator removal):



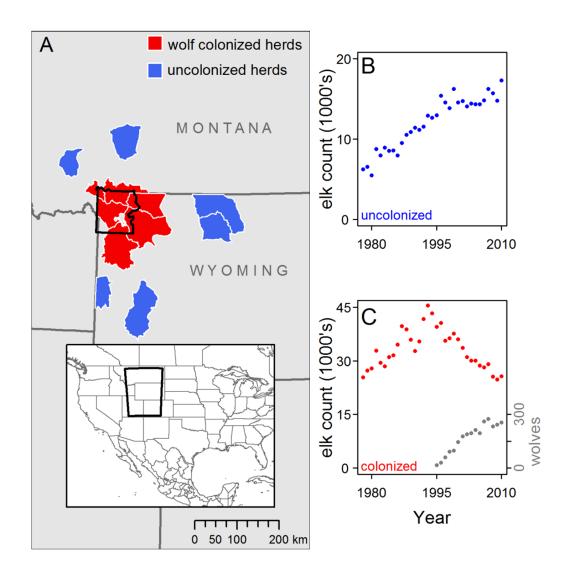
- 1) Equilibrium is perturbed.
- Feedbacks within the system following perturbation cause irruption, then compensatory mechanisms adjust mortality and reproduction, until
- New Equilibrium is attained, at higher density. This could reflect removal of Top-down Forcing, causing state shift to Bottom-up Control.

from Osenberg and Mittelbach (1996)

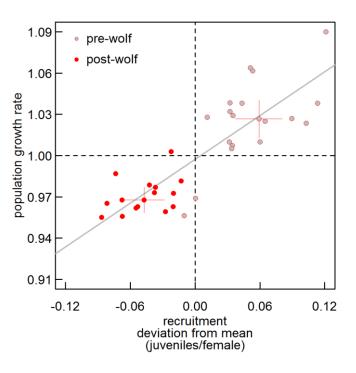
Leopold was right (about release from predation causing irruption of Kaibab deer herd; Binkley et al. 2006, *Ecosystems*). 1906-31 predator removal explains 1st irruption, and 1940s decline in hunting explains second.



NRM elk populations declined following wolf reintroduction only in wolf-colonized elk herds:



Recruitment declined in those herds, and λ fell below 1:

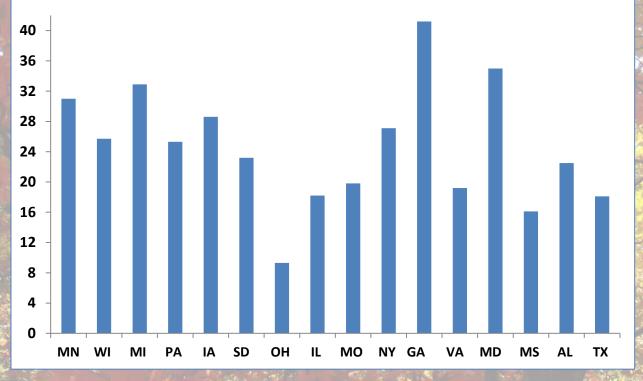


...but, only half the decline due to direct predation (largely compensatory); other half due to "risk effects" such as lower pregnancy rates.

from Christianson and Creel (2014)

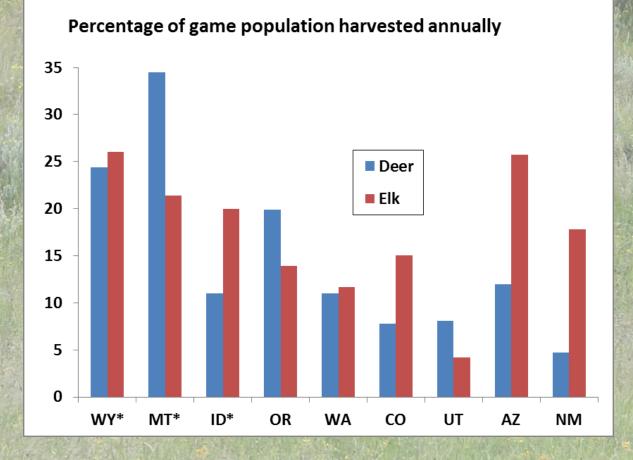
Wolves may limit prey density and growth rate, but... Do wolves decrease deer hunting opportunity in WGL?

Percentage of deer population harvested annually



*3,000 wolves kill 11.5% of Minnesota's deer pop'n annually

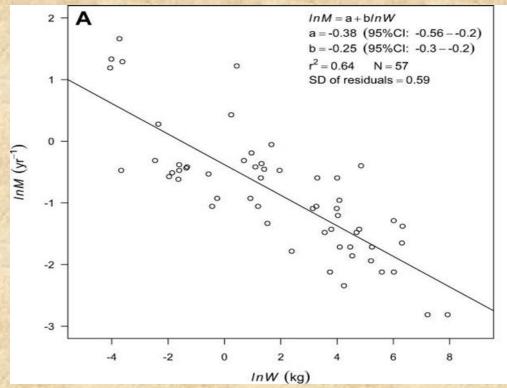
Do NRM wolves decrease elk/deer harvest?



*<u>Note</u>: Colorado has more deer (424,000) and elk (279,000) than Montana & Wyoming combined.

Sustainable harvest mortality?

Charnov and Zuo (2011): "Extinction results if the ratio of the instantaneous mortality rate caused by hunting (F) divided by the adult instantaneous mortality rate (M, for the unexploited population) exceeds a critical value (F/M > C). The C value is determined mostly by the level of **recruitment compensation** as N declines, and C is likely very similar for different sized mammals. We use existing mammal life-history data to estimate C (~0.5). We then estimate the threshold of instantaneous mortality rate, F, as a function of adult body mass, W; it's a -0.25 power allometry."



*Adult mortality for wolves in YNP, on average = ca. 20% (Cubaynes et al. 2014), but annual variation in 95% Cl ranged from 5-50% (higher mortality with higher N due to inter-pack aggression), so threshold F may range from 2.5% to 25%.

Human-caused mortality can be compensatory, additive, or super-additive.

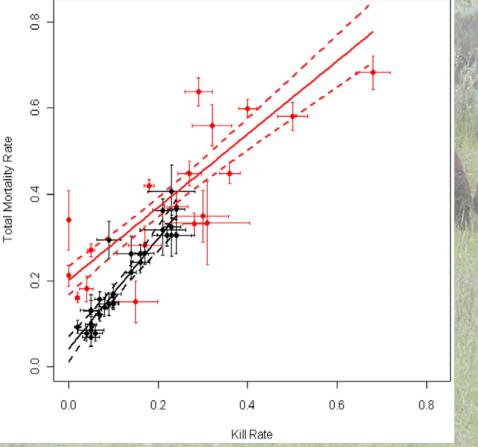
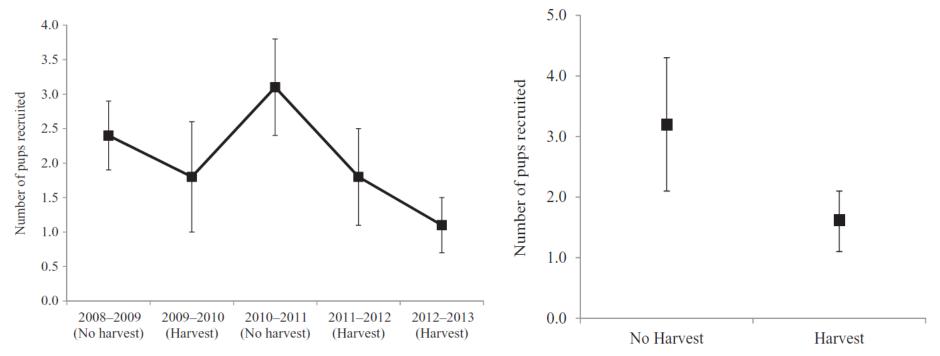


Figure 1. The relationship between total annual mortality and human offtake for wolves in the Northern Rocky Mtns. Recovery Area (black) and other populations (red). Points are annual means for the Northern Rocky Mtns. data, and multi-year means for other populations. The bars on each point show one standard error. The relationships shown are from the bestsupported model in Table 1, a linear relationship with separate slopes and intercepts for the two subsets of data. Dashed lines show 95% confidence bands, accounting for overdispersion by multiplying the variance by the inflation factor (c-hat) from the best-supported model. From Creel and Rotella (2010) doi:10.1371/journal.pone.0012918.g001



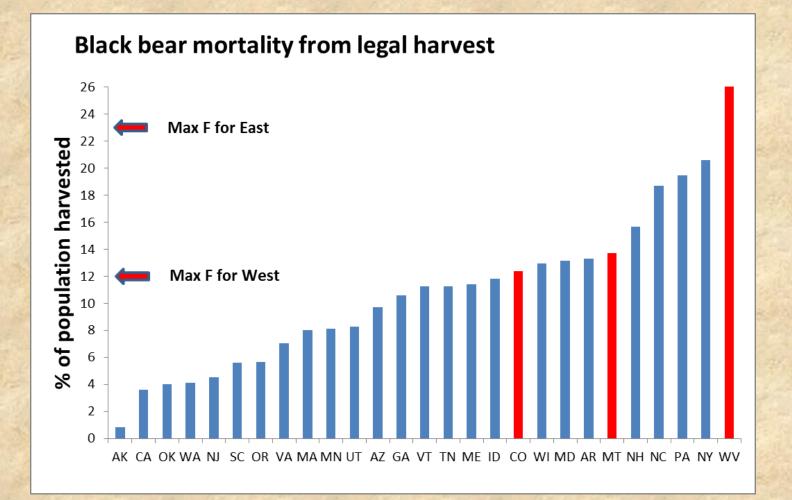
Recruitment in a carnivore before and after harvest

Figure 4 Mean wolf pups recruited by year before and after harvest in Idaho, US, 2008–2013. Errors bars represent SE.

Figure 5 Mean wolf pups recruited before and after harvest in Idaho, US, 2008–2013. Errors bars represent 95% confidence interval.

Recruitment *declined* in NRM gray wolves after harvest; < 1/3 of decline in recruitment was direct effect of harvest; possible indirect effects include infanticide and smaller pack size leading to lower pup survival (*Ausband et al. 2015*)

Black bears in Northwest Montana—max. sustainable total mortality of 12%, yet actual mortality in early 1990s was 25%, mostly due to hunting, and pop'n appeared to be declining (Kasworm and Thier 1994). Yet in Florida, black bears can sustain up to 23% mortality (McCown and Sheik 2013).



Hunting	Estimated					% popu	lation
season	population ^a	Permits issued	Cougars killed ^b	% hunter success	% F	Hunted ^c	Killed
1995–96	35	24	14	58.3	42.9	68.5	40.0
1996–97	42	40	17	42.5	47.1	95.2	40.5
1997–98	33	30	15	50.0	26.7	90.9	45.5
1998–99	26	25	7	28.0	28.6	96.1	26.9
1999–00	21	15	9	60.0	44.4	71.4	42.9
2000-01	15	15	6	40.0	33.3	100.0	40.0
2001-02	17	5	3	60.0	33.3	29.4	17.6
2002-03	20	5	4	80.0	0.00	25.0	20.0
2003-04	22	5	4	80.0	25.0	22.7	18.2
Mean	25.6	18.2	8.8	55.4	31.2	66.6	32.4
SE	3.0	4.1	1.8	17.5	5.0	10.8	3.8

Table 2. Cougar harvest characteristics from Monroe Mountain (Unit 23), Utah, USA, 1996–2004.

^a Estimated number of adults and independent subadults from winter capture and tracking efforts. ^b Legal sport harvest only (Hill and Bunnell 2005).

^c Per capita hunting pressure, i.e., the ratio of the number of permits issued to the estimated population size (column 3/column 2).

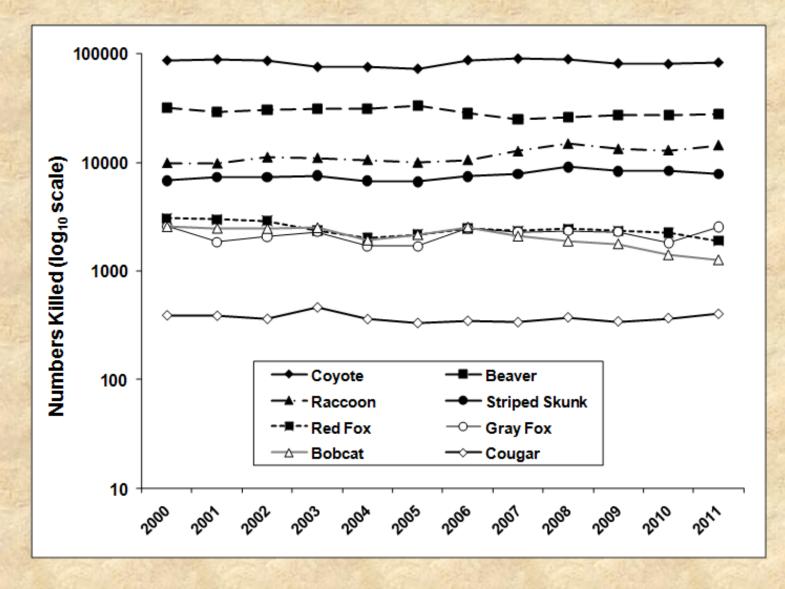
74% of all mortality human-caused (including WS control, roadkill, poaching) from Stoner et al. (2006, J. Wildl. Mgmt.)

Species	USDA/ Wildlife Services kills
Cougar	400
Lynx	0
Bobcat	1,300
Black Bear	570
Grizzly	1
Gray Wolf	365
Coyote	83,200
Foxes	4,600
Raccoon	14,400
Badger	500
Marten	1
Mink	30
Fisher ?	1
Otter	550
Skunk	7,800
All Carnivores	114,000

Annual control kills of carnivores by USDA/WS (2011 annual report)

from APHIS Wildlife Damage annual reports (WS 2015)

Boldface = global pop'n *decreasing* according to IUCN; ? = trend unk.



from Bergstrom et al. (2014, Conservation Letters)

N40561 S-CUB (K. BAER):NV

FOR INTERN	IAL USE ONLY	Aerial S	ada State Program Summary by Property N40561 S-CUB (K. BAER):NV	01/01/20	01/01/2009 to 01/26/2011	
Property	Ferry Hobbs	Flight Hobbs	Qty	Species	Fate	
<u>Ferry Time</u> (Aerial Only)	15.6					
Safety Activities		2.2				
Open Box Arrow Ranches / Open Box Arrow Ranch (Aerial Hunting)		33.8	159 Each	Coyotes	Killed	
2 U Ranch:Nv:32707 / 2 U Ranch (Aerial Hunting)		9.3	37 Each	Coyotes	Killed	
71 Ranch:Nv:32720 / 71 Ranch (Aerial Hunting)		1.5	5 Each	Coyotes	Killed	
7 <u>h</u> Ranch:Nv:32756 / 7h Ranch (Aerial Hunting)		0.2	3 Each	Coyotes	Killed	
Antlpe/Gilbert Cr/Ellison:Nv:7107 / Antlpe/Gilbert Cr/Ellison (Aerial	27	7.0	7 Each	Coyotes	Killed	
<u>Aertai Hunung </u>						
<u>Start Valley</u> (Ndow):Nv:72184 / Starr Valley (Ndow) (Aerial Hunting)		3.2	27 Each	Coyotes	Killed	
T <u>And S</u> Ranch:Nv:32304 / T And S Ranch (Aerial Hunting)		121.9	884 Each	Coyotes	Killed	

Available at https://www.documentcloud.org/documents/2272327-aerial-hunting-ws-nv.html

Species	USDA/ WS	Hunt/Trap ¹	Rate (%)
Cougar	400	3,100	12.5
Lynx	0	5,000	
Bobcat	1,300	56,000	
Black Bear	570	42,000	8-31 ²
Grizzly	1	0	
Gray Wolf	365	1,300	34
Coyote	83,200	451,500	
Foxes	4,600	322,000	
Raccoon	14,400	1,377,400	
Badger	500	12,600	
Marten	1	95,004 ³	
Mink	30	101,600	
Fisher ?	1	7,000	
Otter	550	21,400	
Skunk	7,800	98,000	
All Carnivores	114,000	2,831,000	

Control kills and public harvest of carnivores (2011 annual reports)

Boldface = global pop'n *decreasing* according to IUCN; ? = trend unk.

 ¹to nearest 100, from AFWA (2013)
 ²per state; highest in some eastern states

³as many as 190,000/year in 1980s

What proportion of post-weaning mortality does road kill comprise?

- 48.8% of all adult and post-emergence cub fatalities in UK badgers (Clarke et al., 1998)
- 69.9% of known mortality of otters in Germany, (Hauer et al. 2002)
- 89.5% of Florida black bear mortality (now > 200 per year; FWC 2015. Pop. ca. 3,000; total mort. < 10%)
- ca. 80% of grizzly bear mortality in western N. Amer. is human-caused (combined areas with and without hunting; McLellan et al. 1999; roadkill not listed separately)
- 77% of Florida panther mortality (FWC 2015)
- 28% of puma mortality in S. Calif. (> 62% of all mortality human-caused; Vickers et al. 2015)
- 17% of red wolf mort. 61% of all mort. human-caused (control + poach; Sparkman et al. 2011)
- 8.4% of gray wolf mortality within YNP (Cubaynes et al. 2014)
- Fuller (1989): MN wolves—80% of all mortality human-caused (when NO legal hunting), 11% from roadkill; 10% by other wolves, 10% all other natural causes.
- Non-carnivore e.g. 50% of known mortality of adult female moose in Kenai NWR (Bangs et al. 1989)
 24% of deer in east-central Wisc. (hunter harvest an additional 61%)

Coyotes2	2011					
State	Trap/Hunt	USDA	Est. Pop'n	MaxPop ¹	Min% Killed	Max% Killed
CA	209	2	70,000	404,000	0.1	0.3
OR	5,907	4,084	96,824	254,800	3.9	10.3
WA	0	530	50,000	172,000	0.3	1.1
NV	3,236	5,106	107,920	284,000	2.9	7.7
AZ	774	993	111,720	294,000	0.6	1.6
NM	5,683	5,106	119,320	314,000	3.4	9.0
со	64,294	3,180	102,220	269,000	25.1	66.0
UT	5,296	4,035	80,940	213,000	4.4	11.5
ID	3,838	4,156	81,320	214,000	3.7	9.8
MT	13,169	6,877	143,260	377,000	5.3	14.0
WY	0	7,877	95,380	251,000	3.1	8.3
ND	80,521	3,332	67,506	177,647	47.2	124.2
SD	12,506	2,300	75,000	197,000	7.5	19.7
NE	35,866	2,063	75,620	199,000	19.1	50.2
KS	52,681	33	80,560	212,000	24.9	65.4
ОК	2,949	5,470	67,640	178,000	4.7	12.4
ТХ	0	20,516	257,640	678,000	3.0	8.0
WI	78,519	17	53,580	141,000	55.7	146.6
МІ	27,319	13	55,860	147,000	18.6	48.9
MN	11,130	83	78,280	206,000	5.4	14.3
20-States	403,897	75,773	<mark>1,969,330</mark>	5,182,447	9.3	24.4
All 48	451,533	83,242				
			At same de	ensity		
			as South D	akota		
				¹ =1/km2		

Cougar N							
State	Trap/Hunt	USDA	Other	Est. Pop'n	% Killed		
СА	0	104		4,000	2.6		
OR	315*	117		5,100	8.5		
WA	124	0		1,500	8.3		
NV	134	44		3,000	5.9		
AZ	245	42	7	1,750	16.8		
NM	198	11	50	2,550	10.2		
со	383	16		4,000	10.0		
UT	152**	15		3,000	5.6		
ID	520	2		2,000	26. :		
MT	473	17		2,000	24.		
WY	278	4		2,000	14.:		
ND	18*	0	3	?	?		
SD	71*	0		149	62.4		
NE	4**	0	1	22**	72.7		
14 states	3095	402		28,050	12.5		
Estimates	by Mountai	in Lion Fou	ndatio	n (n/a for T	exas)		
*2013 dat	*2013 data, **2014 data						
NOTE: 5%	NOTE: 5% of SD mort and 10% ND mort = roadkill						

Cougar endangered in SD through 2005

Gray Wo	olf2012-13	5	0			%Δ in Pop
	Trap/Hunt	USDA	Other	Est. Pop'n	%	2011-2013
ID	360	78	30	684	64.0	-11.7
МТ	230	78	29	630	48.9	-4.0
WY	62	28	14	306	29.4	-6.7
WI	11 7	41		809	19.5	-19.0
МІ	0	0		660	0.0	-7.4
MN	413	164		2,211	26.1	?
6 States:	1182	389		5,300	37.6	
	257 in 2013	-14				
*Prince of Wales wolf pop'			n	221	26	-60
(from 2	013 to 2014))				

References

Association of Fish and Wildlife Agencies (AFWA). 2013. U.S. fur harvest 1970-present: Statistics by state, region, and nation.

- Ausband, D.E., C.R. Stansbury, J.L. Stenglein, J.L. Struthers, and L.P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation doi:10.1111/acv.12187
- Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult cow moose on the Kenai Peninsula, Alaska. Journal of Wildlife Management 53:557–563.
- Bergstrom, B.J., L.C. Arias, A.D. Davidson, A.W. Ferguson, L.A. Randa, and S.R. Sheffield. 2014. License to kill: reforming federal wildlife control to restore biodiversity and ecosystem function. Conservation Letters 7: 131-142.
- Binkley, D., M.M. Moore, W.H. Romme, and P.M. Brown. 2006. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems 9: 227-241.
- Boitani. L. 2003. Wolf conservation and recovery, pp. 317–340 in Wolves: Behavior, Ecology, and Conservation, eds. Mech L.D., Boitani L.),. University of Chicago Press, Chicago.
- Cariappa, C.A., J.K. Oakleaf, W.B. Ballard, and S.B. Breck. 2011. A reappraisal of the evidence for regulation of wolf populations. Journal of Wildlife Management 75:726-730.
- Charnov, E. L., and W. Zuo. 2011. Human hunting mortality threshold rules for extinction in mammals (and fish). Evolutionary Ecology Research 13:431–437.
- Christianson, D., and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: A before-after-control-impact approach. PloS ONE 9(7): e102330.
- Clarke, G.P., P.C.L. White, and S. Harris. 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biological Conservation 86: 117–124.
- Creel, S., and J.J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). PLoS ONE 5(9): e12918.
- Cubaynes, S., D.R. MacNulty, D.R. Stahler, K.A. Quimby, D.W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). Journal of Animal Ecology 83:1344–1356.
- Estes, J.A., Terborgh, J., Brashares, J.S. et al. 2011. Trophic downgrading of Planet Earth. Science 333:301-306.
- Fretwell, S. 1977. The regulation of plant communities by food chains exploiting them. Perspect. Biol. Med. 20:169-185.
- Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105:3-41.
- FWC 2015. Black bear roadkill. http://geodata.myfwc.com/datasets/0fc7d491284a4d62b8802a03a68965c0_3
- Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94: 421-425.
- Harris, R.B., C.C. Schwartz, M.A. Haroldson, and G.C. White. 2005. Trajectory of the Yellowstone Grizzly Bear population under alternative survival rates. Wildlife Monographs 161:44-55.

References (cont'd)

- Hauer, S. H. Ansorge, and O. Zinke. 2002. Mortality patterns of otters (*Lutra lutra*) from eastern Germany. Journal of Zoology, London 256: 361-368.
- Janzen, D.H. 1974. The deflowering of Central America. Natural History Magazine 83(4):48-53.
- Kasworm, W.F., and T.J. Thier 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. International Conference on Bear Research and Management 9: 223-23.
- Laliberte, A.S., and W.J. Ripple 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123-138
- Leonard, J.A., C. Vila, and R.K. Wayne. 2005. Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). Molecular Ecology 14:9-17.
- Levi, T., and C.C. Wilmers 2012. Wolves-coyotes-foxes: a cascade among carnivores. Ecology 93:921-929.
- McCown, W., and B. Sheik. 2013. Florida black bear. The Encyclopedia of Earth. Available from http://www.eoearth.org/view/article/152796/
- McLellan, B.N., F.W. Hovey, and J.G. Woods. 1999. Rates and causes of Grizzly Bear mortality in the interior mountains of western North America. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk 2:673-677.
- Morrison, J.C., W. Sechrest, E. Dinerstein, D.S. Wilcove, and J.F. Lamoreux. 2007. Persistence of large mammal faunas as indicators of global human impacts. Journal of Mammalogy 88:1363-1380.
- Mountain Lion Foundation. 2015. Mountain lions in the United States. http://mountainlion.org/us/-us-portal.asp
- Oksanen, L., S.D. Fretwell, J. Arruda, and P. Niemela 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240-261.
- Osenburg, C.W., and G.G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pp. 134–148 in G. Polis and K. Winemiller, eds., Food webs: Interpretation of patterns and dynamics. Chapman and Hall, New York, New York, USA.
- Paine, R.T. 1980. Food webs: Linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49: 666-685.
- Ripple, W.J., J.A. Estes, R.L. Beschta, et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.
- Ripple, W.J., B. vanValkenburg. 2010. Linking top-down forces to the Pleistocene megafaunal extinctions. BioScience 60:516-526.
- Soulé, M.E., J.A. Estes, B. Miller, and D.L. Honnold. 2005. Strongly interacting species: Conservation policy, management, and ethics. BioScience 55: 168–176.
- Sparkman, A.M., L.P. Waits, and D.L. Murray. 2011. Social and demographic effects of anthropogenic mortality: A test of the compensatory mortality hypothesis in the red wolf. PLoS ONE 6(6): e20868.
- Stoner, D.C., M.L. Wolfe, and D.M. Choate. 2006. Cougar exploitation levels in Utah: Implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588-1600.
- United States Fish and Wildlife Service (USFWS). 2015. Gray wolves in the Northern Rocky Mountains. Available from http://www.fws.gov/mountain-prairie/species/mammals/wolf/.
- Vickers, T.W., J.N. Sanchez, C.K. Johnson, et al. 2015. Survival and mortality of Pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLoS ONE 10(7): e0131490.
- Wildlife Services (WS). (2012a) Wildlife damage management. United States Department of Agriculture, Animal and Plant Health Inspection Services. Available from <u>http://www.aphis.usda.gov/wildlife damage/index.shtml</u>.