dressing underlying issues. Alternatives, such as creating a new position within OSTP, are insufficient to navigate complex interagency chains of command.

Last, to mature and learn, oversight institutions must approach governance as a long-term strategic challenge in need of management and research, as well as the involvement of the general public. Investing in interdisciplinary research centers is one way to bring focus to critical risk governance topics like leadership, organization, and learning in a future of distributed biological knowledge and technology. If we do not address the foundational challenge of emergent technologies and biological risk properly, we should expect reactive and poorly conceived restrictions on potentially beneficial research, as well as many more normal "accidents" with increasingly consequential risks to people and the environment, as biotechnology proliferates globally. ■

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Where next? Survival and reproduction of wolves in the Northern Rockies have declined.

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CONSERVATION POLICY

Questionable policy for large carnivore hunting

U.S. wolf-hunting policies do not align with ecological theory or data

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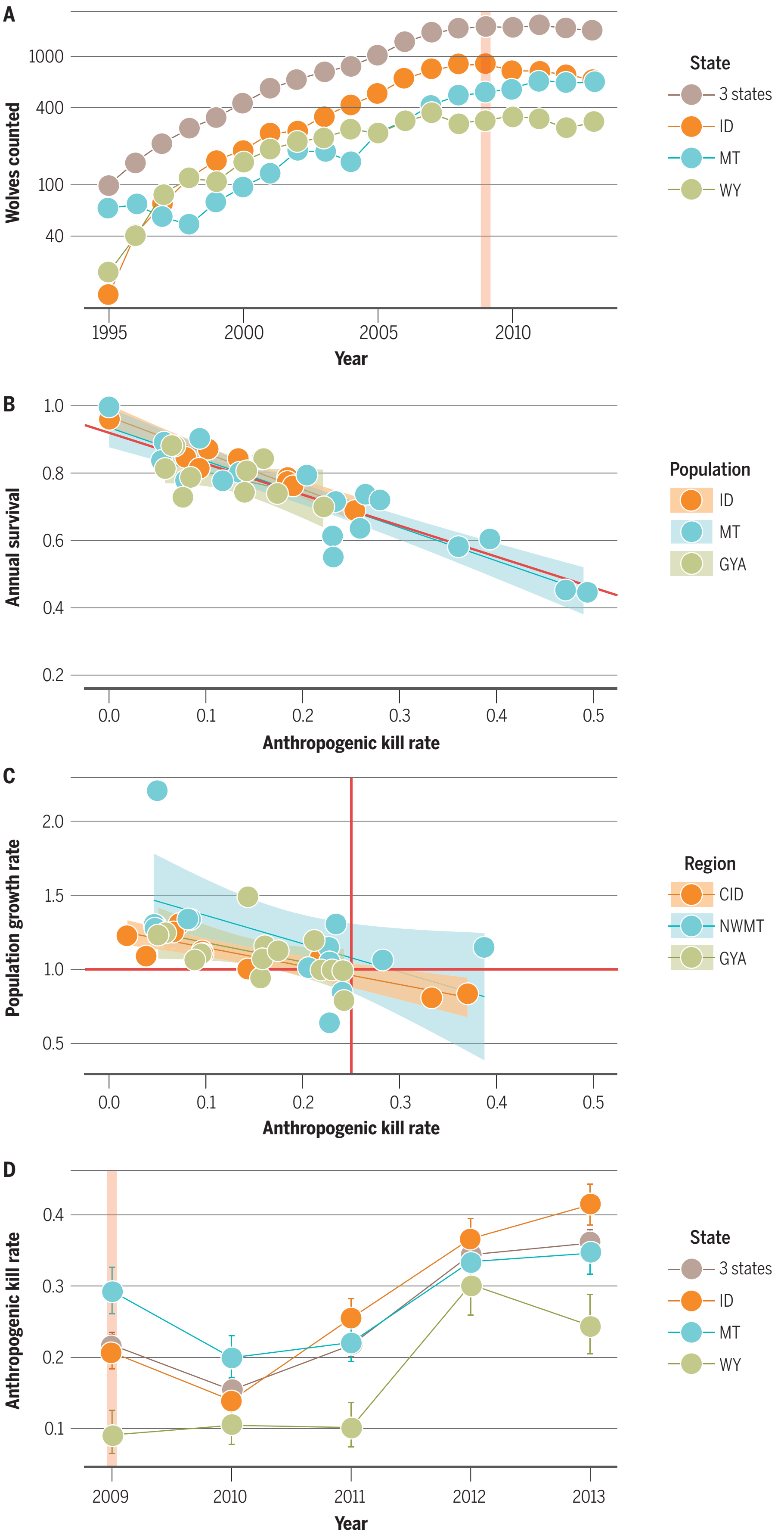
Terrestrial large carnivores are in rapid global decline, with consequences for ecosystem structure and function. Among drivers of these declines, legal hunting is unique because it is intentional and thus relatively easily controlled. Although regulated carnivore hunting potentially reduces conflict and provides revenue for conservation, it can also drive population declines (*1*–*5*). Some policies regulating carnivore hunting address negative effects on demography and population dynamics, but others do not. Here, we use wolf harvesting in the western United States to illustrate four aspects of policy that do not align well with ecological theory and data, and we suggest resolutions.

POLICY

Policies regulating human effects on lions, cougars, leopards, and tigers have responded to research by moving to better evaluate and mitigate demographic costs (*1*, *2*, *5*, *6*). For example, policies for lions (*Panthera leo*) include temporary hunting closures to allow population recovery (*5*) and reduced quotas with sex- and age-limited harvesting (*2*). Nonetheless, hunting policies for large carnivores still often suffer from a lack of science-based guidance. For example, policies for harvest of wolves (*Canis lupus*) in the Northern Rocky Mountains Distinct Population Segment (NRM DPS) suggest that annual harvest of up to 50% of the population has little or no effect on dynamics. Wolves were reintroduced in the mid-1990s, and the NRM DPS grew steadily until 2009 (see the chart, part A). Legal hunting began immediately after removal of the Endangered Species Act (ESA)



Temporal trends in dynamics of wolves. In the original NRM DPS, data were reported by state (ID, Idaho; MT, Montano; WY, Wyoming; or all three states) or regional boundaries (NWMT, Northwest Montana; GYA, Greater Yellowstone Area; CID, Central Idaho), in USFWS population recovery reports (*18*). See SM for details. (**A**) Population counts since wolf reintroduction in the mid-1990s, described by USFWS as minimum number known alive. Red line denotes the onset of legal hunting. Ordinate is $\log_{10}$ scaled. (**B**) Human offtake causes wolf survival rates to decline in an additive manner, with little evidence of compensation. Each point represents 1 year (*8*), and shading shows 95% confidence intervals. The red line denotes completely additive mortality. (**C**) Recent data (*10*) confirm the prior conclusion (*3*) that anthropogenic mortality has an additive (rather than compensatory) effect on annual population growth rates (λ), and that anthropogenic mortality above ~25% typically yields a declining population with $\lambda < 1$. Each point represents 1 year (1998–2014), and shading shows 95% confidence intervals. (**D**) Total anthropogenic mortality has increased substantially since the onset of hunting [denoted with red line as in (A)], doubling within the original NRM DPS between 2010 and 2013, coincident with a shift from steady population growth to gradual decline. Total anthropogenic mortality combines sport hunting with other direct human killing, primarily in response to predation on livestock, and expresses it as a proportion of the population count.

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protections in 2008, occurred in 3 of the 5 years considered here (2009–10 and 2011–13), and continues today. A recent review of current policies by the U.S. Fish and Wildlife Service (USFWS) concluded that harvesting "has not increased any risk" to the NRM DPS (*7*).

Several patterns in the data used to draw these conclusions call them into question (see the chart). We analyze previously published results and information directly reported in USFWS species recovery reports [see supplementary materials (SM)], which have been used as the basis for delisting and increasingly heavy harvest. The issues identified by this analysis are not unique to wolves, and the recommendations that it yields are relevant to other large carnivores.

SIZE, STRUCTURE, DYNAMICS. For wolves (and most other large carnivores), adult mortality rates are low in the absence of human offtake (*8*), which leaves little scope for hunting to substitute for other causes of death (compensatory mortality) (*8*, *9*). Hence, adult mortality rates increase in an additive, nearly one-to-one manner as human offtake increases (see the chart, part B) (*3*, *8*).

Increased adult mortality was correlated with a decrease in wolf pack size since the onset of legal hunting in Montana and Idaho, where pack size declined by 29 to 33% between 2008 and 2013 (*10*). Beyond reducing group size, harvesting mortality can also disrupt social organization (*3*, *4*), and both effects can reduce juvenile survival and recruitment (addition to the population, which depends on litter size and juvenile survival). Pup survival in 10 Idaho packs decreased from 60% in years without hunting to 38% in years with hunting (*11*). Direct trapping or shooting of pups could explain only 27% of this decrease, with the rest attributed to disruption of pack size and social organization (*11*). Recruitment showed a similar decrease in years with hunting, dropping from 3.2 to 1.6 pups recruited per pack (*11*).

Because the population growth rate (λ) is equal to the sum of the adult survival rate and per-capita recruitment, reduced local population growth is inevitable when adult survival and juvenile recruitment decline (see the chart, part C). The mean annual survival of NRM wolves before legal hunting was 0.75 [95% confidence interval (CI) of 0.728 to 0.772] (*12*), so population decline would be expected if recruitment fell below 0.25 recruits per individual (*13*). The mean pack size and recruits per pack reported for Idaho (*10*, *11*) suggest that recruitment dropped below this threshold by 2013, to 0.20 recruits per individual. This would predict population decline even if harvest mortality was completely compensatory. This prediction is corroborated by a 25% decrease in the number of wolves harvested in Idaho and Montana in 2013 (*10*, *14*), despite extended hunting seasons and liberalized hunting limits that have increased the proportion of the population killed (see the chart, part D), a pattern that is commonly taken to indicate that harvest is driving a decline.

BOUNDARIES, DETECTION, GOALS. Several lessons can be learned by considering discrepancies between our analysis and the recent USFWS review concluding that policy has not increased risk to these populations. These lessons are broadly applicable to other exploited carnivores.

Effects of a policy must be considered within the area to which it applies. Carnivore distributions do not follow political borders, but hunting policies do. The relatively constant number of wolves within the entire NRM DPS has been taken as evidence that state-level policies do not increase risk for NRM wolves. However, the DPS originally included only Montana, Idaho, and Wyoming, and has expanded to include wolves in Washington and Oregon. If one evaluates a state's policies by examining effects within its borders, it is reasonable to conclude that risks have increased in some cases. To illustrate, International Union for Conservation of Nature Red List Criterion C1 classifies a population segment as endangered if it holds fewer than 2500 individuals and has declined by ≥20% in <5 years. In Idaho, delisting and subsequent legal harvest produced a 22.4% decline in population counts from 2008 to 2013 (from 849 to 659) (*10*). With no stated population target (other than avoiding relisting under the ESA), current policy does not adequately define a shut-off for this decline.

Evaluation of effects on populations must consider sampling design and effort to control for effects on detection. First, when sampling effort and population counts change in parallel, there is reason to believe that trends in the counts might not describe true dynamics. For example, while the Idaho population count decreased 22.4% from 2008 to 2013, the Montana count increased comparably (see the chart, part A) (*10*), a surprising result given reported decreases in survival (*8*) and reproduction (*11*). During this period, Montana added additional staff and volunteers to monitor the wolf population and initiated a program to gather sightings from the public (eventually with >80,000 reports annually) (*10*). Second, the USFWS evaluation of wolf population trends (*7*) incorrectly asserts that these counts represent "the absolute minimum number of wolves alive." In Idaho, which holds the largest segment of the NRM DPS, tabulated counts are adjusted by substituting mean pack size for smaller pack counts that might have been incomplete (74% of packs in 2013) and then multiplying the adjusted count by 1.125 to account for unseen wolves suspected to be living outside of packs (*10*). Consequently, the Idaho estimate is ~1.75 times the number of individuals known to be alive, and the biggest increase in the minimum estimated NRM DPS occurred in 2006 with the adoption of this method. Recent studies of lions and tigers illustrate the importance of population monitoring that accounts for sampling effort and detection (*5*, *6*).

> ***"policies for harvest of wolves in the Northern Rocky Mountains…suggest that annual harvest of up to 50% of the population has little or no effect…."***

Policy cannot ignore the distinction between local compensation and immigration from an external source population. The suggestion that wolves "can apparently withstand human-caused mortality of 28 to 50% without declining" (*15*) derives from studies [e.g., (*16*, *17*)] in which an external source population was available to provide immigrants to offset local losses (*13*). For lions, harvest mortality outside of national parks affects population dynamics within adjacent parks (*4*, *5*). A clear focus on the distinction between true compensation and source-sink dynamics would improve policy.

Clearly defined, quantitative policy goals are needed for science-based evaluation. Such goals require consideration of population viability and sustainable offtake based on robust science by using all available data. Policies for hunting of wolves in the NRM do not specify maximum harvest or targets for population size or growth (other than avoiding decline sufficient to trigger relisting under the ESA). Well-regulated hunting of large carnivores can yield costs and benefits for conservation but requires attention to both. ■

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SUPPLEMENTARY MATERIALS

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