GENETIC ADEQUACY of GREATER YELLOWSTONE GRIZZLY BEARS

(The Introduction to "Endangered Genes of Yellowstone" should be read before this section.)

Yellowstone grizzly bears, now the southernmost on the continent, declined to about 200 animals in the 1980s. They have been isolated from other bear populations for over 100 years. They have increased steadily in number and distribution during the past 25 years, with over 600 bears today. With their limited number and isolation, the genetic diversity of GYE grizzly bears is among the lowest for populations in North America (Kamath et al. 2015). Genetic heterozygosity and allelic variation per locus appear to have been declining slowly for many decades (Miller and Waits, 2003; Kamath et al. 2015), but the rate of decline may have slowed recently.

Measured long-term (since 1910) and medium-term (since 1960 or 1985), measurements of downward trends for allelic diversity of GYE bears (Miller and Waits, 2003; Kamath et al., 2015) usually do not reach a level of scientific certainty, for which the usual standard is less than a 5% chance an observed trend is due only to sampling variation. However, with several statistical tests across different sets of genetic data, the overall evidence for declining genetic diversity is stronger than the evidence for stable genetic diversity. Wildlife management decisions cannot depend solely on a standard for scientific "certainty", especially when the future of an important and irreplaceable population is at risk. Evidence for declining genetic diversity of GYE grizzlies, both theoretical and observed, should not be ignored.

If GYE grizzly bears are removed from the Endangered Species list, the near-term future of GYE bears will be determined by the delisting/conservation Strategy of the Fish and Wildlife Service, and its application according to state bear management plans in Idaho, Wyoming and Montana. In the Strategy (USFWS, 2016), almost all criteria for the future of GYE grizzly bears involve numbers of bears, with little reference to population quality. The future of the bear genome is inadequately considered (pp. 51-53).

Discussion of genetic drift is vague and inadequate. While one recent estimate of the genetically-effective population size is 469 bears (p. 52), the Strategy fails to note the

imprecision of this estimate (Confidence limits are 284-772, Kamath et al. 2015:5512) and does not recognize other, lower, estimates in the same and other sources. Moreover, the Strategy proclaims that 469 bears "approaches a minimum threshold" of 500 that Franklin (1980) once proposed as sufficient to retain adequate genetic variation. Recent published disagreement with this threshold and support for a genetically-effective population of 1000 or more (Frankham et al. 2014; Traill et al. 2010) are ignored.

There is nothing about the future of natural vs. artificial selection. Aside from gradual loss of alleles, inevitable with proposed population levels, artificial selection and drift will alter the quality of the grizzly bear genome – rearranging the combinations of alleles as they are distributed among animals and as they determine the broad ecological fitness of the population to a dynamic, wild environment.

The Strategy presents a confusing set of lower limits, goals and management triggers for maintaining the GYE grizzly bear population size. The Strategy concludes (p. 52) that, with "current population levels", genetic factors do not pose a "substantial" risk to the viability of GYE bears. However, management emphasis is on numbers of bears, not on the quality of the bear genome. Further, the Strategy does not commit to maintaining current population levels.

The Strategy proposes to maintain an estimated population of "around" 674 bears, using hunting to assure sufficient mortality to offset recruitment. However, the Strategy sets a lower limit of 500 bears; it may allow hunting down to a population of 600 bears (though not in Yellowstone National Park); and the killing of "conflict bears" will remain discretionary with the states, whatever the population size.

Outside the "Demographic Monitoring Area" (essentially the GYE), including all the potential habitat where alleles from the northern continental divide population could travel to the GYE, maintaining and augmenting the GYE bear genome, bear mortality will be discretionary, whatever the number of bears in the GYE. This discretionary mortality will be based upon two Montana FWP plans.

These plans are for western Montana (Montana Fish, Wildlife & Parks, 2006) and for southwest Montana (Montana Fish, Wildlife & Parks, 2013). Neither plan adequately discusses the issue of genetic quality of a bear population. In the latter plan, "Goals for the Grizzly Bear" (p. 6) do not include maintaining genetic quality (but see next paragraph). Issues to be addressed to achieve goals (p. 6) do not include genetics or monitoring of genetic qualities of populations. Failure to list genetic quality as an up-front goal or issue suggests an uncertain commitment from Montana.

Montana (FWP 2013:49) asserts it is a long-term goal to allow bears in southwest and northwest Montana to reconnect through maintenance of "non-conflict" grizzly bears. However, this plan fails to note that hunting, including of non-conflict bears, will be contrary to achieving this goal. Moreover, hunters will be required to avoid taking sows with cubs. In a small population, expected in the anticipated corridor between the GYE and northern populations, this harvest strategy may increase the preponderance of related bears in any intermediate (or "stepping-stone") population, thereby fostering inbreeding and limiting genetic diversity for "reconnection" bears (Allendorf et al. 2008).

The FWS Strategy summarizes Montana's uncertain commitment to provide for bears, and alleles, to travel from the northern continental divide population to the GYE (pp. 52-53). We are told there will be an "opportunity" for non-conflict bears to move; that

stepping-stone populations would "likely be facilitated"; and that FWP "anticipates" that needed bear movements will be "allowed". While removal of conflict bears will be a priority, there is no real commitment for natural or artificial genetic support of the GYE grizzly population.

Montana proposes (FWP 2013) that genetic connectivity between bears in the GYE and the northern continental divide area will eventually occur as "non-conflict" and "socially-acceptable" bears will be allowed to move through a difficult (for bears) landscape where conflict bears will be removed and some non-conflict bears will be taken by sport hunting. How long this reconnection may take, if it occurs, is not is not addressed in the Montana plan.

I note that, Miller and Waits (2003) recommended transfer of bears from the northern continental divide population to the GYE over 13 years ago. They suggested that immigration or transplant of 1-2 bears per 10 years from the northern Continental Divide grizzly population into the GYE will maintain current levels of genetic diversity. However, there are contrary opinions (Mills and Allendorf 1996, Vucetich and Waite 2000). For a population as important as GYE grizzly bears, for which risks should be minimized, it seems wrong to apply the lowest possible standard that can be rationalized, rather than a safer standard based on all the available biology.

However, grizzlies in the northern population have since been captured and handled by FWP. But no bears (presumably "non-conflict" bears) have been translocated to the GYE (pers. comm. Kerry Gunther, YNP). This does not engender faith in FWP's commitment to or anticipation of genetic support for the GYE bears.

As noted above, three genetics concerns for the future of GYE grizzly bears are inbreeding, genetic drift, and the effects of selective forces of the environment. With proposed future population sizes, inbreeding will be a minor problem, at most (Kamath et al. 2015:5512, 5514). However, there has been and will continue to be a slow loss of alleles due to genetic drift. (my interpretation of Kamath et al., Table 1 and comment on p. 5514: "there will inevitably be loss" of alleles from a future population maintained at "around" 674 bears; and there must have been a loss of alleles during the past many decades from populations that were much smaller, at least since 1985). Loss of alleles due to genetic drift has and will continue to compromise the future evolutionary potential of GYE bears. In addition, a preponderance of drift and artificial selection over natural selection may allow an accumulation of mildly deleterious alleles, gradually degrading the bear genome to an uncertain degree.

Hereafter, I concentrate on the role of artificial (vs. natural) selection in contributing to drift: that is to loss of alleles and to rearranging alleles away from combinations established in the original wild genome.

The mechanisms of natural selection in grizzly bears are not well understood. After the age of 1 or 2 years, almost all the natural selection (competition and mortality) of grizzly bears results from intraspecific strife. Most natural mortalities are bears killed by other bears.

Adult males often kill juvenile bears and sometimes other adult males. Removal of adult males, with bear control or sport hunting, can cause spatial reorganization and increased killing of cubs by adult males (Leclerc et al. 2017). Limited evidence indicates that sows, especially sows with cubs, select feeding sites to avoid adult males. Reproduction by

sows can be inhibited by the presence of other nearby females.

The overall role of competition/avoidance behavior in determining access of individuals to the best habitats, and therefore to survival and lifetime reproduction, is unclear. However, the wild bear genome has developed through natural selection and competition has been a major arbiter of that selection. Natural selection will be necessary to maintain the wild genome, including the ecological fitness of a population to its wild environment.

For post-juvenile bears, the relative effectiveness of natural selection can be assessed by comparing amounts of natural vs. artificial (human-caused) mortality for each sex. Of course, all bear deaths, especially natural deaths, are not detected. Estimates for the number of bears killed due to human and natural causes are very imprecise and depend on uncertain assumptions in the analysis (Cherry et al. 2002). For 2014 and 2015 combined, it is crudely estimated that 39% of adult female mortalities were human-caused and that 61% of adult male mortalities were likewise artificial (Annual Reports, Interagency Grizzly Bear Study Team, 2014, 2015).

The number of human-caused bear mortalities has been increasing in recent years. This trend has been at least partly due to expansion of the bear range outward from YNP. A growing proportion of the bear population occurs in areas where conflicts are likely and bears are controlled. In addition, after delisting there will be mortality of bears, including non-conflict bears, due to sport hunting.

Artificial mortality of bears will be most pronounced in the area between the GYE and the northern continental divide population of bears. This is the hoped-for corridor where non-conflict bears are to be allowed to provide genetic support for GYE bears. Likely, the percentage of artificial (vs. natural) mortality within the corridor will be greater than cited above. The corridor may become a genetic filter, ultimately supplying bears with diminished wild genomes to interact with GYE bears.

Impacts of this artificial selection on the wild bear genome are uncertain. We should expect bears to become less aggressive, mobile, curious and exploratory. Essentially, we are selecting for a more domestic bear that can live in a more domestic environment. Abundant, if not preponderant, artificial selection will replace natural selection for valuable wild characteristics of anatomy, physiology and behavior. These may include energy efficiency, competitiveness, hibernation physiology and very many little-known and unmeasured characteristics bequeathed from past evolution.

As proposed in the FWS Strategy, the GYE grizzly bear population is not and is unlikely to become genetically adequate in the foreseeable future. Loss of alleles, accumulation of mildly deleterious alleles, and rearrangement of alleles due to drift and replacement of natural selection, especially for males, will gradually diminish qualities of the wild bear genome. Implications of this trend are unclear.

The future portends little or no genetic connection between GYE grizzly bears and those in northwest Montana. Genetic connection will depend upon the bear management policies of Idaho and Montana. Current policies provide a core of bear numbers and genetic quality only in YNP, surrounded by a "sink" for both bear numbers and for alleles associated with wildness.

For managing and conserving this unique bear population in the most important, large and irreplaceable wild ecosystem in the United States, we should be erring on the side of bear

conservation, not seeking a compromise that emphasizes or even approaches minimum viability with an uncertain degree of decline in wild population quality. However, considering their conflicting nature, we may decide not to live with a genetically adequate wild population of grizzly bears. If so, we should at least acknowledge the implications for the wild bear genome.

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