Conservation Genetics Resources
https://doi.org/10.1007/s12686-022-01262-7

PERSPECTIVES

A greater yellowstone ecosystem grizzly bear case study: genetic reassessment for managers

Craig L. Shafer[1]

Received: 6 September 2021 / Accepted: 18 March 2022

Abstract
There are five grizzly bear (*Ursus arctos horribilis*) populations in the lower 48 states of the United States. My goal in this Commentary was to ascertain whether genetic diversity is being lost from the isolated GYE grizzly bear population and to better understand any viability implications. I reviewed the scientific literature, including two key genetic studies that the US Fish and Wildlife Service (USFWS) relied upon for their 2007 and current 2017 GYE grizzly bear genetics policy. I discovered that some studies reveal a loss of heterozygosity in the GYE bear population, both historically and in recent decades. Some had a statistically significant depletion rate. My review took place periodically between 2010 and 2021 and indicates that the genome of the GYE grizzly bear population is too small for long-term adaptation. The paper includes a discussion about evolutionary adaptation which invokes time frames rarely considered by nature conservation planners. I also examined genetic statements in the USFWS's 2017 GYE grizzly bear delisting regulations and highlighted those that seem incongruent with current scientific thought. If this paper is read by some scientists, land managers, administrators, environmentalists, and others with some genetics background, they will better understand some USFWS decisions and policy statements. This case study illustrates that land management agencies can provide a one-sided treatment of some science when writing regulations about genetics.

Keywords Effective population size · Evolution · Genetics · Greater Yellowstone Ecosystem · Grizzly bear · Migration · US Fish and Wildlife Service

Introduction

At present, there are four distinct grizzly bear populations in the U.S. lower 48 states, consisting of the Greater Yellowstone Ecosystem (GYE; 20,000 km^2 with 737 bears), the U.S. portion of the Northern Continental Divide Ecosystem (NCDE; 25,000 km^2 with 1068 bears), the U.S portion of the Selkirk Mountains area (3021 km^2 with 53 bears), the Cabinet-Yaak area (6700 km^2 with 55–60 bears) and the Northern Cascades Ecosystem (25,000 km^2 with 0 bears) (USFWS 2021) (Fig. 1). Additionally, wildlife biologists familiar with the Selkirk-Bitterroot-Frank Church River-of-No-Return Wilderness Complex (SBFW; 15,054 km^2) acknowledged sightings of two transient bears over the last 13 years with another five confirmed within 15 km or less of this recovery area (personal communication, Montana Fish, Wildlife & Parks, and USFWS). There exists 358,000 km^2 of human-dominated, mostly non-protected land separating the GYE, NCDE, and SBFW. The distance between the GYE and NCDE grizzly bear populations is approximately 110 km (White et al. 2017).

The GYE grizzly bear population was removed from the "threatened" list on July 31, 2017, on the basis of provisions of the 1973 US ESA (16 U.S.C. 1531–1544, 87 Stat. 884, as amended). However, the grizzly bear was returned to the ESA listing by a Federal District Court judge on September 24, 2018. This was the second time a federal judge refuted all the US Fish and Wildlife Service (USFWS) reasons for delisting this bear population. The final USFWS decision to delist the GYE grizzly bear on April 30, 2007, and again on July 31, 2017, was based primarily on demographic population data; however, genetics data were also taken into account. For more information about the study area, US grizzly bear distribution and population status, and ESA history, see Part I of the case study.

✉ Craig L. Shafer
cshafer@gmu.edu

[1] George Wright Society, P.O. Box 65, Hancock, MI 49930-0065, USA

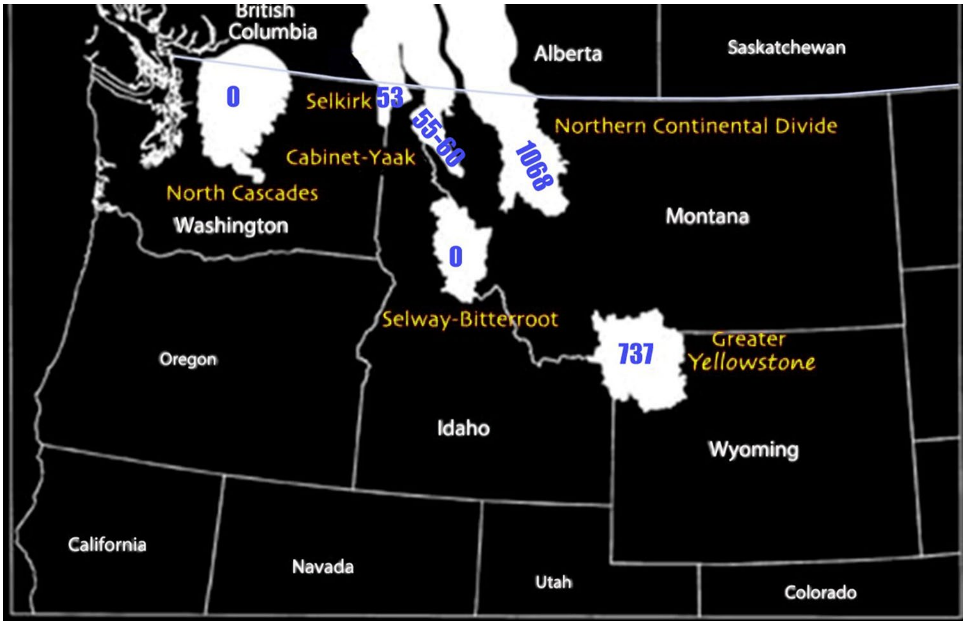

Fig. 1 Lower 48 grizzly bear populations as of 2021. Habitats shown in white based on Servheen et al. (2002); population numbers from USFWS (2021)

This work, spanning 2010 to 2021, addresses my concern about whether the GYE grizzly bear population is losing genetic diversity, how much, and what is the viability implications. This suspicion of potential ongoing genetic problems followed from an understanding that habitat loss and fragmentation generally result in a decrease in the number of alleles as well as a reduction in observed and also expected heterozygosity in mammals (Lino et al. 2019). To also address my question in a policy context, I assessed the USFWS's treatment of genetics in its proposed 2007 and final 2017 regulations to remove the GYE grizzly bear Distinct Population Segment from the Endangered Species Act (ESA) "threatened" list (USFWS 2007, 2017). I also reviewed USFWS responses to public comments on the regulations since they also reflect USFWS thinking. With only a modest familiarity with genetics, some scientists, bear managers, administrators, environmentalists, and others who try to review the USFWS 2017 federal delisting ruling, may be stymied by the jargon and the complexity of the pertinent genetic studies. The message that Schonewald-Cox et al. (1983) conveyed 38 years ago remains relevant: technical literature must be explained so practitioners and others can understand more of it.

I proceeded by reviewing the scientific literature and then evaluated USFWS statements in their 130-page, 2017 final grizzly bear regulations (USFWS 2017) that pertain to genetics. This review indicates that land management or regulatory agencies can provide a one-sided treatment of some information when it comes to genetics. This paper is therefore warranted to see how some federal genetics policies for the GYE grizzly bear can be misrepresented and what impact that might have on the bear. This paper is a continuation of work started in Shafer (2013).

Since many non-geneticists understandably have a limited grasp of population genetics and evolution, this review might be described as "translational ecology" (Schlesinger 2010). That is, translating the scientific literature so that others with different or less technical backgrounds can understand it. In the words of Groom et al. (2006, p. 626), "It is impossible to integrate conservation science into environmental policy if no one but the scientist understands the science."

Genetics background

It is important to be somewhat familiar with certain aspects of conservation genetics to better understand this paper. What follows are highlights.

Habitat fragmentation negatively impacts individual genetic fitness and the overall population viability of many species (Young and Clarke 2000; Lindenmayer and Fischer 2006). Studies have reported a positive correlation between a population's heterozygosity (*H*) level and its fitness (Allendorf and Leary 1986; Mitton 1993; Reed 2005); however, see the Genetic Fitness Section in the Appendix for newer insights. Loss of genetic variation resulting from decreases in *H* and allelic diversity (*P*) (Avise 1994), is caused by habitat fragmentation and population isolation (Keyghobadi 2007).

Corridors are presumed to reduce the negative impacts of habitat fragmentation, such as the loss of genetic variation (Christie and Knowles 2015). Some studies have documented the use of corridors by animals (Gilbert-Norton et al. 2010; Resasco 2019).

Inbreeding results in increased homozygosity or decreased heterozygosity (H). The negative influence reduced heterozygosity has on populations is well documented (Frankham 2010). Inbreeding is found in some outbreeding plants and animals (Lacy 1997) and for example, in brown bears in Nordic zoos (Laidre et al. 1996). Inbreeding depression (F) is the negative outcome of inbreeding. A rapid decline in fitness has been observed in zoo populations (Ralls and Ballou 1983) due to inbreeding and has also been detected in wild animals (Keller and Waller 2002). When measured in various wild mammal populations, F was moderate to high (Crnokrak and Roff 1999). Small population size encourages inbreeding, increasing the number of individuals that are homozygous for deleterious recessive alleles (Wright 1977) while larger populations have greater genetic diversity (Frankham 1996).

Gene flow between isolated populations reduces the frequency of homozygous genotypes (Wahlund 1929) and therefore the potential impact of deleterious alleles. The continuous infusion of new alleles, even in large populations, helps to ensure that enough genetic variation is maintained to prevent extirpation or extinction (Frankham et al. 2010).

Genetic erosion has a negative influence on most species declining toward extinction (Spielman et al. 2004) and can often lead to their demise (Frankham 1995b). The probability of species extirpation or extinction due to genetics was deemed to be a minor concern in the past (Lande 1988; Caughley 1994), but many do not hold this viewpoint today (e.g., Frankham 2005c; Brook 2008). An “extinction spiral” accompanies a decline in genetic diversity and can result in local population extirpation (Gilpin and Soulé 1986).

Model approaches for assessing the genetic diversity of a population

Adequate population size

In 1995, the US District Court for the District of Columbia remanded (sent back) the USFWS’s treatment of genetics isolation on grizzly bear populations to the agency for further study. However, by September 21, 2009, the Court deferred to USFWS’S expertise in judging “adequate population size” (Greater Yellowstone Coalition v. Christopher Servheen 2011). Thus, the determination of adequate population size was left to agency discretion. The USFWS used effective population size (N_e) in its consideration of what an “adequate population” would be for GYE bears.

Effective population size

Effective population size (N_e), an idea introduced by Wright (1931), is the best concept for predicting the rate of loss of genetic variation in isolated populations. N_e, therefore, is the key factor used to monitor or manage a population’s genetic variation. It is defined as “the number of individuals that would result in the same loss of genetic diversity, inbreeding, or genetic drift if they behaved in the manner of an idealized population” (Frankham et al. 2010, p. 530). That is, “ideal” refers to a hypothetical population with a constant size, equal sex ratio, and no immigration, emigration, mutation, or selection. Simply, N_e is an indicator of a population’s evolutionary potential and risk from inbreeding (Franklin and Frankham 1998).

N_c is always larger than $\mathrm{N_e}$ except in very unusual situations. The larger the N_e, the smaller the loss of genetic variation. In other words, a larger N_e retains more genetic diversity, since the rate of genetic drift and the loss of genetic diversity will be lower at a larger N_e value. Effective population size (N_e) (the number of breeding individuals needed for long-term adaptation) is therefore different from the total, or census population size (N_c). Wang (2005) warned that N_e is “notoriously difficult to estimate” and described various concepts of $\mathrm{N_e}$: inbreeding effective size (N_{ei}), variance effective size (N_{ev}), eigenvalue mutation effective size, and coalescent theory effective size (Ewens 1990; Gregorious 1991; Caballero 1994; Whitlock and Barton 1997; Charlesworth et al. 2003). N_{ei} and N_{ev} are the most used, where N_{ei} indicates how much H changes over time due to inbreeding, while N_{ev} is a measure of changes in allele frequency due to genetic drift. Wang (2005), Wang et al. (2010), and Palstra and Ruzzante (2008) reviewed the various approaches to estimate N_e. Despite recent advances in measuring N_e (Luikart et al. 2010), there remain various pitfalls in its calculation (Hare et al. 2011; Palstra and Fraser 2012).

The 50/500 rule: population size needed to diminish genetic erosion

The 50/500 rule was derived from a literature review by Franklin (1980) and Soulé (1980). Franklin (1980) recommended a N_e of at least 50 individuals for short-term genetic fitness for single and independent populations, such as vigor, fecundity, fertility, and disease resistance. This number was derived from the work of animal breeders who found that fewer than 50 individuals caused an unacceptable 1% loss of H per generation due to inbreeding. Franklin (1980) also recommended a N_e of 500 individuals to prevent the erosion of genetic variation and allow for long-term adaptation, as did Soulé (1980). Franklin’s estimate was derived from work on *Drosophila* bristle number (Lande 1976). It was also based on the assumption that the loss of genetic variation at $N_e = 500$ will be balanced by a gain through mutation, an assumption that has been questioned (Lacy 1992). Soulé (1987, p. 175) later, and with some reluctance, reaffirmed his guess at $\mathrm{N_c}$: the order of magnitude lower population boundary would be "low thousands" for a 95% chance of persistence, without any fitness loss, for several 100 years.

The 50/500 rule was accepted by some scientists (Newmark 1985; Wilcox 1986) but later fell into disfavor with others (Lande 1988; Boyce 1997). Frankham et al. (2014) recommended revising the 50/500 rule to 100/1000. Franklin et al. (2014) retorted that the Frankham et al. argument was unconvincing. Jamieson and Allendorf (2012) recommended 2000 for long-term evolutionary fitness but this all depends on the adopted ratio for N_e/N_c. Therefore, after more than three decades, the $N_e = 500$ value for long-term fitness has not been abandoned by some scientists (Franklin et al. 2014; Jamieson and Allendorf 2012) though boosted upward by others. A few authors mentioned connectivity in their N_e discussions (Frankham et al. 2014; Jamieson and Allendorf 2012) but none explicitly stated that N_e applies to both single and connected populations. Fifty years ago, Frankel (1970, p. 166) suggested that healthy population sizes demand "a thousand rather than hundreds."

Genetic variation in GYE grizzly bears

Proctor et al. (2005), Proctor et al. (2012)) used a likelihood-based test to find area-specific allele frequencies and employed 15-locus microsatellite genotyping to find an average expected heterozygosity (H_e) in GYE bears of 0.64 to 0.67. They confirmed the genetic distinctiveness of the grizzly bear populations in the western US and Canada and attributed it to isolation.

Paetkau et al. (1998) used approximations for eight *mtDNA* loci that revealed 69% H in the NCDE population, but only 55% in the GYE population. There was a 15–20% reduction in H for the GYE population during one hundred years and an F of 1–4%. They observed that the GYE population exhibited among the lowest genetic diversities of any brown bear population in continental North America.

Waits et al. (1998) used both *mt*DNA and nuclear microsatellite analysis for 220 brown bears over North America. Using samples from DNA depositories (GYE 53 bears, NCDE 49 bears), they found a genetic diversity (h) of 0.611 for NCDE bears which dropped to 0.240 for GYE bears. Note: h, defined by the authors as genetic diversity, equals H for nuclear genes but not for mtDNA. This drop was not statistically significant in the GYE though the authors characterized it as "considerably lower" than for the NCDE.

Miller and Waits (2003) discovered a slight but not statistically significant decline in H from the 1910s (0.580) to the 1990s (0.560). Allelic diversity grew from 4.50 (1910s), to 4.63 (1960s) to 4.88 (1990s). Historical samples used eight dinucleotide microsatellites. Contemporary data came from Paetkau et al. (1998) and other sources.

Haroldson et al. (2010) used nuclear genetic protocols. They adopted 16 microsatellites obtained from 424 bears sampled from 1983 to 2007, including eight identified by Miller and Waits (2003). They found a 67% H for NCDE bears which declined to 60% for GYE bears. This 7% H drop was less than the 14% H drop derived by Miller and Waits (2003).

Kamath et al. (2015), whose authors included Interagency Grizzly Bear Study Team (IGBST) members, used three methods to determine N_e. They examined 20 microsatellites, including the eight used by Miller and Waits (2003), but came to a very different conclusion: no changes in H or P from 1985 to 2010.

Except for Miller and Waits (2003), all these workers assumed that the genetic diversity in GYE and NCDE bear populations was once the same until the effects of isolation manifested. The Miller and Waits (2003) and Kamath et al. (2015) studies will now be examined in detail because of the influence they had on USFWS policy.

The scientific basis for USFWS genetics policy

Miller and Waits (2003): initial findings, the debate, and follow-up policy

Miller and Waits (2003) examined tissue samples from 110 bears in museum collections deposited from 1912 to 1920 (28), from 1959 to 1981 (72), and from 1992 to 1999 (136). Using these historical samples, Miller and Waits (2003, p. 4338) found that the H of GYE grizzly bears "declined slightly" from the 1910s to the 1990s. This drop was later judged as statistically significant (Allendorf et al. 2006). They also estimated that P was 4.50 in the 1910s, 4.63 in the 1960s, and 4.88 in the 1990s so P increased slightly over this period. They also calculated H at 55% for the GYE which was lower than the NCDE's 69%. They characterized genetic diversity in the GYE bears as "significantly lower" than in the NCDE population (Miller and Waits 2003, p. 4334). In addition, they found an inbreeding rate of 2.3% per generation.

They reported very low estimates of N_e (~85 for 1910–the 1960s and ~75–89 for 1960–1990) and indicated the upper and lower bounds of the mean N_c from 1965 to 1995 to be 180 and 454, respectively. Based on evidence that N_c was at least 400, and using earlier models and other studies, Miller and Waits (2003) estimated N_e to be 108 in 2003 and thought their data supported the notion that the lower genetic diversity in the GYE grizzly bears resulted from the population drop they experienced in the early 1970s (Allendorf et al. 2006). They used a N_e/N_c of around 0.3. Based on their findings, in 2007, the USFWS planned to implement translocations by 2020 and every 10 years thereafter (USFWS 2007); which apparently never took place.

Miller and Waits (2003) asserted that genetic factors were unlikely to have a significant impact on the viability of the GYE grizzly bear population over the next several decades but they also said gene flow would be beneficial. They later clarified that the projection timeline for needed genetic infusion to be "20–30 years" (Allendorf et al. 2006).

Another scientist, John Ballou, using models, predicts only a minor H loss over time. With a current N_e of say 80, inbreeding will increase at only about 0.0006 per generation [1/ (2*N_e)] (J. Ballou, Smithsonian Institution's National Zoological Park [retired], personal communication, October 2016). Yet another scientist also predicted minor H loss. Allendorf et al. (2019) calculated a GYE grizzly bear H loss of 0.005 every 10 years given a population of 500 grizzly bears and assuming a N_e of > 100. But two other scientists argued, "there is no safe amount of inbreeding for normally outbred organisms" (Frankel and Soulé 1981, p. 72). H varies from 0.0 to 0.26 in mammals, with a mean of 0.04 (Sinclair et al. 2006).

Based on Miller and Waits (2003), the USFWS asserted that the GYE grizzly bear population required a N_e of only 100 bears to maintain their fitness, despite estimates by some other geneticists that N_c in the range of 2000–4000 bears would be needed to maintain genetic variation for future adaptation (Lynch and Lande 1998; Sinclair et al. 2006). Miller and Waits (2003) indicated that if the GYE grizzly bear population N_e ever rose to 500, and assuming a N_e/N_c of 0.27, then an $N_c > 1850$ would be required for long-term adaptation. Miller and Watts, therefore, made both short-term recommendations (N_e as 100, which would demand an N_c of > 400) and long-term recommendations ($N_c = 1850$). However, the USFWS focused on the short-term recommendation.

Scientists expressed their concern regarding the USFWS's basis for judging the required N_e and signed a letter to the USFWS on March 20, 2006. Those scientists believed that the GYE grizzly bear population needed a N_e of 500 (or an N_c of 2000–3000 bears) before enough genetic diversity would be available to withstand random, regional-scale events (Craighead et al. 2006). Furthermore, in 2002, the consensus of the contributors to the book *The Role of Genetics in Population Viability Analysis* (Allendorf and Ryman 2002) decided that an N_c of 500 individuals was too small to support the long-term genetic fitness of a population.

In addition, commenters regarding the early USFWS 2007 proposed rule (2007 *Federal Register* notice) suggested that the goal for the GYE grizzly bear population (N_c) should also consist of 2000–3000 bears. If not, they argued that movement corridors connecting the GYE population with other bear populations should be created (USFWS 2007). Despite these suggestions and those of the above scientists, the USFWS decided that an N_c of 500 individuals was sufficient for delisting. The USFWS also believed that the GYE grizzly bear population was "close to carrying capacity inside the DMA (demographic monitoring area)" which to them was 700 bears (USFWS 2017, p. 30,571). Yellowstone National Park resource managers adopted the Miller and Waits (2003) recommendations (United Nations Educational, Scientific and Cultural Organization 2011).

The above recommendations are not the largest for N_c. Some scientists are convinced that estimates for N_e/N_c are 0.1 for species in general (Nunney and Campbell 1993; Vucetich et al. 1997; Frankham 1995c; Frankham et al. 2010). If so, any estimate for N_c would be 10 × higher than N_e, not just 4 × higher using a N_e/N_c ratio of 0.25. Lande (1995) estimated N_e as 5000 to retain evolutionary potential, which Frankham et al. (2010) thought was too high. Lynch and Lande (1998) estimated that N_e would vary between 1000 and 5000 bears. Allendorf and Ryman (2002) reviewed these recommendations in detail.

Kamath et al. (2015): findings and revised genetics policy

The USFWS in 2007 indicated they would provide updated guidance for GYE grizzly bear management if future genetic data challenged its policy (USFWS 2007). New information from a study instigated and conducted by the IGBST surfaced in 2015. Kamath et al. (2015) used three methods to determine N_e. Using a single sample nuclear approach, they examined 20 microsatellites in 729 live bears, including the same microsatellites used by Miller and Waits (2003) and others. They also used two multiple sample approaches to estimate variance N_e (N_{ev}) and inbreeding N_e (N_{ei}).

One of the techniques used was estimation by parentage assignment (EPA), as described by Wang et al. (2010). Kamath et al. (2015) recalculated Miller and Waits' (2003) historical N_e estimates and found that N_{ei} had greatly increased from ~ 80 during 1910–1960 to ~ 280 at that time. They estimated that from 1984 to 2007, N_e/N_c was 0.42–0.66, a fourfold increase. Their adopted 0.42–0.66 ratio was very different from a computer simulation value of 0.24–0.32 (Harris and Allendorf 1989; Allendorf et al. 1991). Kamath et al. (2015) believed that N_{ei} for the GYE grizzly bear population increased from 102 in 1982 to 469 in 2010, and pointed out that H levels measured by other scientists actually increased: 0.55 in 1998 (Paetkau et al. 1998), to 0.56 in 2003 (Miller and Waits 2003), and then to 0.60 in 2010 (Haroldson et al. 2010). However, the results were not statistically significant. During the 2017 *Federal Register* public comment period, some argued that the new EPA method of genetic assessment needed more review (USFWS 2017b, p. 30609).

Kamath et al. (2015) found no changes in H or P from 1985 to 2010. They calculated an inbreeding coefficient (F) of only 0.2% for 1985–2010, in contrast to an F of 2.3% per generation for 1985–1999 obtained by Miller and Waits (2003). The USFWS subsequently questioned whether the changes in H were "biologically meaningful" (USFWS 2017, p. 30,623) and proposed withdrawing their translocation plans in 2016 (USFWS 2016). Other scientists were not hesitant to comment on the genetic diversity differences they observed in these studies. Based on data from allozyme loci, microsatellite loci, and *mt*DNA, Allendorf et al. (2006) concluded that the GYE grizzly bears had "substantially less" genetic variation compared to NCDE bears and the drop was statistically significant. These judgments diverge from the manner the USFWS portrayed the Miller and Waits (2003) findings: "there is no evidence for a 'shrinking gene pool'" (USFWS 2017, p. 30,610). Kamath and colleagues said the GYE grizzly bear population would benefit from gene flow, as did Paetkau et al. (1998), Waits et al. (1998), Miller and Waits (2003), and Haroldson et al. (2010).

The USFWS embraced the findings of Kamath et al. (2015). As a result, the US Geological Survey (USGS) issued a press release indicating that the GYE grizzly bear population had not suffered a significant loss in genetic diversity (US Geological Survey 2015) and would therefore not suffer any important loss in genetic variation with a population size of 640–797 individuals. It asserted that the number of individuals was "sufficient to assure long-term genetic viability." Reading the same Kamath and colleagues' paper, an NGO issued a press release that stated that GYE grizzly bear genetic diversity had been stable since the 1980s, with an inbreeding rate of only 0.2%, so translocation was unnecessary (Anonymous 2015). The USFWS accepted the conclusions of various scientists that natural dispersal would benefit the GYE bears genome (USFWS 2017, p. 30,536). However, the USFWS nevertheless indicated that translocation would only occur if there were demonstrable negative impacts to the bears because of lowered H. But after citing Miller and Waits (2003) and Kamath et al. (2015), the USFWS continued to assert that "genetic concerns are not a threat to the GYE grizzly bear population" (USFWS 2017, p. 30,536). The US Forest Service (USFS) (2006, p. 68) believed the GYE grizzly bear population was already viable. The USFWS supported this USFS position: "there is more than enough [GYE] habitat to support a viable population" (USFWS 2017, p. 30,511).

Of key importance, however, is that government scientists and managers working in the GYE by 2003 had adopted calculations that address only *short-term* genetic fitness and not *long-term* genetic vigor. Furthermore, some regulations and other statements indicate that the USFWS does not understand N_e. For example, a statement in a USFWS strategy report (USFWS 2016) indicates the agency misapplied the Kamath et al. (2015) study. After referring to the Kamath et al. (2015) claim that N_c is 460, the agency believed this value was close to the 500-value espoused by Franklin (1980) for long-term evolutionary fitness. However, Franklin (1980) was referring to $N_{e,}$ not N_c, so an N_c of 500 bears is much too small to achieve long-term genetic fitness. The criticism about misunderstanding N_e was a common complaint in the USFWS 2017 rules comments. "Other commentators took issue with our calculation and analysis of effective population size" (USFWS 2017, p. 30,609). More examples of misinterpretation follow.

Based on Kamath et al. (2015), the USFWS maintained that N_e for GYE grizzly bears is more than 4 × the minimum N_e calculated by Miller and Waits (2003). However, Miller and Waits (2003) were discussing short-term fitness when they said that existing N_e is likely to be "near or more than > 100." The USFWS then mischaracterized what Miller and Waits (2003) said and suggested using $N_e = 100$ as the new yardstick for overall genetic fitness (USFWS 2017). However, Miller and Waits (2003) and Kamath et al. (2015) clearly observed that the GYE grizzly bears do not meet the population standard for long-term genetic fitness. The current USFWS's goal is to maintain a total population of 500 bears in the DMA based on short term genetic fitness (USFWS 2017b, p. 30,610). But long-term genetic fitness is the ideal.

A planning time frame of a hundred years is not uncommon for species viability analyses as the USFWS pointed out (USFWS 2017, p. 30,561). A several 100-year time frame would be moving in a direction to retain genetic variation long term *if* the bear population size provided enough genetic diversity for adaptation. The agency mentioned minimum viable population size (e.g., Trail et al. 2007) only once in the regulations but without definition, discussion or projection. One scientist deemed it impossible to do a population viability analysis for even the best-studied bear species in the world, the grizzly bear (Boyce et al. 2001).

There is one inconvenient truth about these studies that warrant mention. No agreement about the accuracy of microsatellite data exists (Balloux and Lugon-Moulin 2002) and there are limitations to such methods (Putman and Carbone 2014). Although molecular markers are assumed to be substitutes for quantitative genetic variation, that correlation is weak (Reed and Frankham 2001). Storfer (1996) and others suggest that the use of quantitative variation would be a better approach. These grizzly bear genetic studies used neutral markers, such as microsatellites, which do not code for functional proteins and therefore do not consist of the genetic material used in natural selection. Therefore, we should not unquestionably accept these study results based on neutral genetic variation (McKay and Latta 2002). Nevertheless, that is all we have to guide us for now. Allendorf (2016) treats the history of various approaches used to determine the genetic composition of individuals and populations.

Summation

Compared to the NCDE, the GYE population is losing *H* (Paetkau et al. 1998; Waits et al. 1998; Miller and Waits 2003; Haroldson et al. 2010). This drop is statistically significant (e.g. Miller and Waits 2003, cited in (Allendorf 2006). However, Kamath et al. (2015) found no decrease in *H* or *P* from 1985 to 2010. Some models predict only a minor loss in *H* due to inbreeding. When comparing *H* differences between GYE and NCDE bears, some IGBST members (White et al. 2017) simply said the differences were "relatively large."

However, *H* is not the most important factor here, even though it was emphasized by the USFWS and the IGBST. For example, the agency thinks low *H* decreases the ability to adapt and evolve (USFWS 2017, p. 30535, 30515). *H* loss is less significant than the loss of *P* (Petit et al. 1996), and the latter will be lost more quickly (Keyghobadi 2007). Genetic drift will cause a loss of alleles and possibly retain (fix) the deleterious ones. Heterozygosity does not tell us much about allelic diversity (Allendorf 1986), so reliance on *H* values indicates little about the potential for long-term adaptation. Management for *H* by itself is misguided because the removal of *P* is more critical to a genetically diverse population (Fuerst and Maruyama 1986). A review of fragmentation studies found the most marked result was the loss of alleles, while measures of *H* and the number of polymorphic loci were less prominent (Schlaepfer et al. 2018). One rules commentator made a reasonable suggestion: create a model of the rate of allele loss at different population sizes resulting from genetic drift (USFWS 2017, p. 30,609).

Perhaps in the future, we can calculate how much genetic diversity will be retained based on population sizes or habitat area/protected area configuration (Méndez et al. 2014). For now, if the GYE remains isolated, numerous scientists indicate it is too small to retain grizzly bear genetic variation over the long term.

As this case study outlines, some USFWS statements in the 2017 regulations are of concern. As a review, the USFWS (2017) remarked that: N_e was 100 for GYE bears and N_c was 469 (p. 30,610), there is uncertainty about whether the GYE bears "differ markedly" from the NCDE population (p. 30,519), *H* values indicate that GYE bears will continue to remain "healthy" (p. 30,535) and translocation into the GYE would occur only as a "last resort" (p. 30,536). Thus, according to the USFWS, genetic isolation is "not a threat" to the GYE grizzly bears in the "foreseeable future" (p. 30610). Not surprisingly, one rules commenter asked the USFWS to define the foreseeable future (USFWS 2017, p. 30,607).

For an elaboration on four key-related genetics concepts and their relationship to USFWS genetic policy statements, see the "Appendix". We now will expand our "time frame of concern" (Frankel 1974).

A neglected concern: evolutionary adaptation

There are claims that fast genetic changes have taken place in a variety of short-generation species like birds (e.g., date of arrival at nesting grounds) due to changes in climate (Rice and Emery 2003; Bradshaw and Holzapfel 2006; Scheffers et al. 2016). Resistance to antibiotics and insecticides represent another example (Georghiou 1986). However, adaptation usually requires long periods of time (Barnovsky and Kraatz 2007). Regardless, the potential for evolution is a function of the amount of usable genetic diversity (Fisher 1930). More specifically, quantitative genetic variation is the key ingredient for adaptation albeit the least known and hardest to measure (Frankham et al. 2004). Endangered species generally have less genetic diversity than species that are not endangered (Frankham 1995a). One scientist (Weeks et al. 2011) made a distinction between translocations for increasing the fitness of a small population and those to maintain its adaptive potential. A rules commentator suggested making projections about the evolutionary health of the GYE grizzly bears (USFWS 2017, p. 30,609).

Disregarding the need for genetic diversity to support the evolutionary process represents only a short-term, and arguably a shortsighted management perspective. That short-term perspective is typically the need to access and counter the effects of inbreeding. A long-term perspective involves the need to retain evolutionary potential and yet management planning by US Federal land managing agencies is often guided by documents designed for 15–20-year time-spans. This approach is illogical today. Hence, movement corridors or translocations in perpetuity are needed for what Pulsford et al. (2015) called "evolutionary process connectivity."

Addressing future climate change, for example, demands that we ensure that populations have ample genetic diversity to allow for future genetic modifications (Holt 1990; Hoffman and Sgrò 2011; Beston et al. 2015; Sgrò et al. 2011; Weeks et al. 2011). But we also need to be aware of Holt's (1990, p. 314) warning: "Predicting the microevolutionary consequences of climate change for even a single species is dauntingly complex."

Land managers need to incorporate more long-term evolutionary biology concepts into their management strategies (Lankau et al. 2011; Cook and Sgrò 2017a). There is a lack of knowledge among today's land stewards on evolutionary theory (Smith et al. 2014; Cook and Sgrò 2017b; Taylor et al. 2017; Cook and Sgró 2019).

The global challenges we currently face demand that we do not ignore evolutionary biology principles (Carroll et al. 2014). Such insufficient knowledge was observed in this case study. Understanding the importance of genetics and evolutionary potential is critical to ensure successful biodiversity conservation, and thus we must facilitate collaboration with genetic experts or encourage training opportunities for managers charged with genetic decision making. As Frankel (1974) admonished, our society should "acquire evolutionary responsibility."

Management implications

The population size goal for the GYE grizzly bear population should be at least the lower threshold value needed to provide ample genetic variation for the long term. This corresponds with a planning framework of hundreds of years (Shaffer 1992; Bader (2000). The continual infusion of new alleles into even a large population will help ensure ample genetic variation and prevent extinction (Allendorf et al. 2013). If grizzly bear dispersal between the GYE and NCDE seems impossible, a translocation strategy may have the same result as maintaining a much larger N_c in one area (Weeks et al. 2011), for example, 2000–5000 bears in the GYE. An N_c of 2000–5000 individuals will likely be sufficient over the long-term assuming a N_e/N_c ratio of around 0.25 (Jamieson and Allendorf 2012; Frankham et al. 2014; Allendorf et al. 2019). However, the USFWS said, "We disagree with the suggestion that there must be 2500 to 5000 grizzly bears throughout the 48 states" (USFWS 2017, p. 30,558). Many scientists cited in this case study disagree with the USFWS on this point, even if one only considers the GYE population.

As of 2018, the IGBST regards the GYE grizzly bear ecological carrying capacity in YNP to be full (Van Manen et al. 2019) which reflects an earlier research judgment (Schwartz et al. 2006). Based on my calculations here, while using the N_c estimates by genetic experts ($N_c = 2000$–5000 bears), and *assuming* a carrying capacity of 700 bears (Haroldson et al. 2010), the required number of individuals in the GYE for optimal genetics over the long terms is roughly 3–7 times greater than Haroldson and colleagues' 700 individuals.

Therefore, the following USFWS statement is decidedly not true: "suitable habitat, including fragmented and unfragmented areas, contains the habitat necessary for a healthy and viable grizzly bear population in the long term" (USFWS 2017, p. 30,588). The proximity of other bear populations and habitat corridors/connectivity are critical components of any long-term conservation strategy. Another rules commentator said what should now be obvious: "connectivity or lack thereof has the potential to impact this population's [GYE] genetic fitness" (USFWS 2017, p. 30,579). A long-term genetic perspective (i.e., 100 years and more) may sound like an unrealistic "ivory tower" recommendation, but a similar one is needed today for climate change. Hannah and Salm (2005) recommended that protected area management plans for climate change include 30–50 and 80–100-time horizons. As a well-known National Park Service (NPS) historian remarked, NPS "natural resources management seems usually not to have been thought of in truly far-reaching time spans" (Sellars 1997, p. 308).

The periodic infusion of new genetic material through translocation may be our best conservation option for retaining genetic diversity in the GYE grizzly bear population. However, we should nevertheless continue efforts to retain or recreate habitat connectivity between the GYE, NCDE, and the SBFW. As Frankham et al. (2004, p. 134) remarked, "Genetic management of fragmented populations is the greatest unmet challenge in conservation genetics."

Lest we forget, Frankel (1970) and later Franklin (1980) recommended that our primary management goal should be the recovery of populations of a size that allows evolution by natural selection to continue. The GYE grizzly bear population provides an opportunity to manage these bears relying on such early genetic insight and all that has followed.

To repeat, the following guideline for long-term genetic fitness is based on the advice of some respected conservation geneticists (Jamieson and Allendorf 2012; Frankham et al. 2014; Allendorf et al. 2019): an N_c of 2000–5000 individuals will likely be sufficient over the long-term assuming a N_e/N_c ratio of around 0.25. Land managers need to seek out meta-analyses, consult geneticists regarding periodic regional analyses, or ramp up their own genetic expertise.

Appendix: Elaboration on four genetic concepts

Genetic drift

Genetic variation is maintained in a population due to the interaction of four factors: gene flow, mutation, genetic drift, and natural selection (Lacy 1987). A concern not emphasized by USFWS is the impact of genetic drift on the loss of genetic diversity. Genetic drift can overcome natural selection and result in the slow assembly of deleterious mutations (Hare et al. 2011). This is called genetic load (Wallace 1970). If mutation continues, it is referred to as mutational meltdown (Lynch et al. 1995). Theory predicts that allelic diversity in small populations will be lost at the rate of half the N_e per generation (Wright 1931), but must be accompanied by numerous unrealistic assumptions about the population. The effect of inbreeding in small populations occurs more slowly than does the impact of genetic drift (Leberg 2005), nor does inbreeding result in a loss of alleles (Jamieson 2009). Allendorf (1986) agreed that P is more significant for future evolutionary potential than is H. Gene flow remains necessary to support genetic diversity for long-term adaptation. Natural selection is probably happening and at a very much reduced rate in the GYE population since it is so small. Whatever genetic changes happen to the population will be due to genetic drift—random changes—not natural selection. This would be an argument for translocation sooner rather than later (J. Ballou, personal communication, November 2016). The fixation of alleles through genetic drift could manifest even in populations of moderate N_e (Avise 1994) or for populations of any size (Allendorf et al. 2013). As Allendorf and Ryman (2002) explained, inbreeding is not always essential to cause a loss in fitness. However, genetic drift can cause alleles to be lost and reduce H (Leberg 2005).

Translocation

When and if grizzly bear translocations (a form of genetic rescue) are conducted by the USFWS, approximately 1–10 migrants per generation who successfully breed will be needed to compensate for any genetic variation loss due to small population size (Mills and Allendorf 1996) which Wang (1984) supported. An earlier 1986 USFWS workshop (Allendorf and Servheen 1986) recommended at least one migrant per generation. Some workers indicate that more than ten individuals may be needed (Vucetich and Waite 2000). At this level of migration, the loss of P and H will be minimal while still allowing for intrapopulation divergence in allele frequencies. After an isolated population of greater prairie chicken (*Tympanuchus cupido*) declined from 2000 in 1962 to < 50 by 1994, genetic diversity and egg production dropped. But after birds from a large genetically diverse population were translocated into the remnant population, egg viability returned (Westemeier et al. 1998). A single wolf (*Canis lupus*) immigrant infused genetic diversity into a genetically depauperate population (Vilá et al. 2003).

The migration of one or more breeding individuals per generation can achieve a balance between the four genetic diversity factors (gene flow, mutation, genetic drift, and natural selection) whatever the size of the receiving population. This counter-intuitive result indicates that integration of new adaptive alleles into the receiving population's gene pool will occur rather quickly (Barton and Hewitt 1989), though Varvio et al. (1986) warned that it may take decades. Translocation is required to maintain the genetic diversity of the GYE bears and to allow for possible adaptation to climate change and other factors that may threaten their long-term survival. Thus, the purpose of translocations is to increase genetic diversity and allow for adaptation (Weeks et al. 2011).

Genetic fitness

The USFWS believes that the GYE grizzly bear population is fit due to observed normal litter sizes, no apparent evidence of disease, high rates of survivorship, an equal sex ratio, normal body size and physical characteristics, and a stable-to-increasing population size (USFWS 2017, p. 30535). However, such USFWS observations of perceived bear fitness do not ensure that the population is not weakened as a result of reduced genetic variation. For example, some subtle adaptations would be difficult to observe such as behavioral changes, more hemoglobin to compensate for increasing altitude, or new enzymes to adjust to for different diets (Frankham et al. 2017). Fitness has been defined as including survival, disease resistance, growth and developmental rate, and developmental stability (Allendorf and Leary 1986). But there is disagreement by other scientists on what constitutes fitness (Ariew and Lewontin 2004). Furthermore, the expression of survival abnormalities due to genetic impoverishment can manifest long after genetic changes occur (Lacy 1997). Thus, there is a need for genetic monitoring to measure changes in H and sub-population introgression (De Barba et al. 2010) which the USFWS is doing using genetic tags like described by Lamb et al. (2019).

However, some scientists are skeptical of the relationship between H and fitness (Lynch 1996; Paige 2017). A meta-analysis by Reed et al. (2003) showed that the relationship explained only 15–20% of variation in fitness. Another animal meta-analysis by Chapman et al. (2009) revealed only a small positive relationship. Other results were inconsistent (David 1998; Hansson and Westberg 2002). Correlations between heterozygosity and inbreeding were strong only when around 200 loci were examined (Balloux et al. 2004). In spite of such results suggesting a declining positive relationship, DeWoody et al. (2021) emphatically argued that genetic diversity is tied to overall fitness. Some populations have survived for hundreds of generations with low genetic variation (Reed 2010), but they lack the alleles for adaptation (Linløkken 2018). Population bottlenecks often lose rare alleles (Denniston 1978). Bottlenecks of short duration may have little influence on heterozygosity but can cause a severe reduction in alleles (Allendorf 1986).

Outbreeding depression

The concept of outbreeding was first described by Dobzhansky (1948). A genetic dilemma remains because we do not always know whether translocation is the best strategy for sustaining genetic variation. Although a population can benefit from the infusion of genetic diversity, the introduction of new alleles can also dilute existing local adaptations and taxonomic integrity and result in outbreeding depression. Genetic swamping can occur when locally adapted genes are disrupted by gene flow (Shafer 1990, 2001; Storfer 1999; Tallmon et al. 2004). Weeks et al. (2011) developed an outline to assist in decision-making. The dilemma described resulted in one scientist concluding that “no unassailable generalizations are possible” (Vergeer et al. 2018), while another described the conflict as “being between a rock and a hard place” (Edmunds 2007, p. 463). This long-standing problem warrants further research (Whiteley et al. 2015). Nevertheless, according to Frankham (2010) and Love Stowell et al. (2017), the fear of diluting the genetic integrity of a population or species through outbreeding depression could provide land stewards with an excuse for avoiding genetic management actions whose outcomes were uncertain. In situations where the probability of outbreeding depression was low, when inbred populations were outcrossed there was a positive genetic outcome in 92.9% of the 156 cases reviewed (Frankham et al. 2011). Hence, the fear of outbreeding depression appears to have been overstated (Hoffmann and Sgrò 2011).

As a result of their review, Frankham et al. (2011) suggested that if two populations are genetically similar, occupy similar habitats, and have been isolated for less than 500 years, then the probability of outbreeding depression is minor. One laboratory experiment illustrated that the negative effect of losing genetic diversity was not due to inbreeding, but rather was based on a decreased ability to adapt (Frankham et al. 1999). Therefore, the probability of harmful outbreeding depression occurring after translocating grizzly bears between the GYE and NCDE is not the concern that Templeton (1986), for example, thought it was for species in general. Outbreeding depression is often temporary (Frankham et al. 2017).

Acknowledgements J. A. Shafer provided feedback on all paper drafts. C. M. Schonewald was a sounding board for many of my ideas. I thank my university committee for support: E.C. Parsons, L. M. Talbot, T. E. Lovejoy, and J. C. Kozlowski. Other university professors and classmates commented on the paper: V. A. Buckley-Beason, R. G. Kroner, F. B. Herta, and C.L. Romelo. I thank J. D. Ballou for reading an earlier version of the manuscript. Many anonymous reviewers provided helpful comments on the paper and my gratitude to them is profound.

Funding No funding.

Data availability Any data not in the manuscript are available from the author.

Declarations

Conflict of interest The author(s) declare that they have no competing interests.

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