Genetic augmentation of grizzly bears in the Greater Yellowstone Ecosystem: Pilot Program

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INTRODUCTION

The Yellowstone Ecosystem Subcommittee of the Interagency Grizzly Bear Committee proposes adopting a process that would assist the long-term genetic health of the grizzly bear population in the Greater Yellowstone Ecosystem (GYE) via the occasional translocation of non-conflict grizzly bears from the Northern Continental Divide Ecosystem (NCDE). This document lays out the processes required to allow this to occur, how we envision field operations to follow from that, and also provides the biological rationale for taking this action. A more detailed step-down providing guidance for field operations is also included. This is consistent with the commitments made by the States of Montana, Wyoming, and Idaho

Briefly, biologists have long recognized the long-term risks that wildlife populations face when they are isolated from other populations. The importance of ultimately providing biological connectivity between bears in the GYE and those further north has been recognized for many years (e.g., Allendorf and Servheen 1986). Because both the GYE and NCDE populations of grizzly bears have expanded in abundance and distribution, they are closer to becoming connected via natural movements of bears than at any time during at least the past 50 years. Natural movements of bears into the GYE have been recognized as desirable by Montana Fish, Wildlife and Parks for many years (Dood et al. 2006, MFWP 2013:41), management zones committed to by federal and state managers are intended to facilitate occasional migration (NCDE Subcommittee 2021), and conflict prevention and reduction activities continue that may ultimately allow these movements to occur.

Similar programs have been considered in the past but not yet implemented. The “Final Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area” of March 2007 (since superseded by the one signed by participants in December 2016) noted that migration of grizzly bears into the GYE could occur either via natural movements or artificial transplantation. In the proposed delisting rule of 2007, USFWS pledged to “*continue efforts to reestablish natural connectivity, but our partners…* [presumably including MFWP]*… will transplant one to two effective migrants per generation if no movement or genetic exchange is documented by 2020*…”. USFWS further stated that “*Augmentation is proposed as a precautionary measure based on the recommendations of Miller and Waits (2003, p. 4338) to maintain* *current levels of genetic diversity, should grizzly bear movement into the GYA not occur over the next 20 years*."

The USFWS (2021:181) also contemplated possible translocation, suggesting confidence that "*…translocation, if necessary, will address the ability of future GYE bears to adapt evolutionarily*". Regarding accountability and monitoring, USFWS (2021:181) stated that "*The IGBST also monitors genetic diversity of the GYE grizzly bear population so that a possible reduction in genetic diversity will be detected and responded to accordingly with translocation of grizzly bears into the GYE originating from another population in the lower-48 States. In addition to possible translocations, measures described in the 2016 GYE Conservation Strategy are and will continue to be used to promote genetic connectivity through natural movements. These measures include habitat protections, population standards, mortality control, outreach efforts, and adaptive management*."

BACKGROUND

Grizzly bears living in the Greater Yellowstone Ecosystem (GYE) have been isolated from other grizzly bear populations for possibly over 100 years, and their continued genetic isolation is a long-term conservation concern. The rate of inbreeding has been very low (0.2% over 25 years), and no inbreeding effects have been detected. Additionally, effective population size has increased well above the level where short-term genetic effects would be expected, and is approaching criteria for long-term population viability. Nonetheless, with lower genetic diversity than other North American grizzly bear populations, it is recognized that infusion of genetic material from other populations would enhance the adaptive capacity and long-term persistence of the GYE population. Although no evidence of immigration has been documented since genetic monitoring began, the potential for natural movement into the population by bears from the Northern Continental Divide Ecosystem (NCDE) is increasing over time. Due to population growth and expansion, distance between the nearest portions of estimated occupied ranges of these two populations to each other had diminished to only 57 km by 2020.

One option for increasing genetic diversity in the GYE is to assist the natural immigration process via occasional human-aided translocation of bears from the Northern Continental Divide Ecosystem. However, translocation of bears, especially between populations separated by human-dominated landscapes, is not without risks. Not all translocated bears survive or settle in the release area. Translocated bears often exhibit unusual movement patterns, likely motivated by their homing instinct or because of spatial competition from resident bears and difficulty in finding a vacant space to settle. Post-translocation movements of grizzly bears can be extensive, often increasing their mortality risk (e.g., vehicle collisions, poor nutrition) or the likelihood of encountering human settlements and engaging in human-bear conflict. If human-aided translocation is implemented, an imperative is to minimize the probability that translocated bears come into conflict with people.

If a translocation option is acceptable to cooperating agencies, careful planning with respect to selection of candidate individuals, timing, and locations will help decrease these risks and increase the likelihood of successfully adding to the genetic diversity of the GYE population.

This working document is intended to guide field practitioners (and to inform wildlife managers, land managers, and the interested public) regarding our collected expertise on 'best practices' likely to result in success. Ultimately, successful implementation would entail translocated bear(s) staying within the GYE and producing or siring cubs that themselves survive long enough to attain survival rates comparable to resident bears. Documenting such success, however, is likely to be a difficult and long-term process, will require statistical procedures such as assignment tests based on DNA samples. More immediate metrics of success, such as documenting an individual's fidelity to the new location, will help inform future translocation procedures (if needed).

We emphasize that the objective of any translocation of grizzly bears into the GYE is for ensuring that genetic diversity is sufficient to provide long-term evolutionary potential. The objective is not to increase population size in the GYE generally.

PROCESS CONSIDERATIONS

Whether or not migrant grizzly bears move into Yellowstone and ultimately contribute genetically, FWP, in cooperation with others, can undertake measures that would, if successful, have a similar biological effect. Process considerations include:

1. FWP would, on an on-going and continuing basis, translocate conflict-free bears from other populations in Montana to pre-selected and pre-approved areas within the GYE. Areas chosen for release would be those judged most likely to allow individuals to meet their biological needs without conflicts with humans, and also most likely to encounter and breed with individuals of the opposite sex.
2. Trapping would be conducted to capture and move bears as resources allow.
3. The sex/age of bears that would be augmentation candidates, exactly where they would be released within the GYE, and whether there are times of year when augmentation would be inadvisable are biological considerations that are crucial to the ultimate success of the initiative. Those considerations are discussed in greater detail below.
4. Bears whose presence is deemed to have greater biological value to the source population than the GYE would not be considered candidates for this program.
5. FWP or USFWS staff in northwestern Montana would coordinate with counterparts in the GYE on the details of transportation and release.
6. The frequency with which such animals would become available would vary annually, and not be predictable. The expectation is that approximately 2 to 4 candidate bears would become available and be moved every 10 years. There would be no additional expectations or requirements for the timing beyond that. For example, if opportunities presented themselves, > 1 bear might be moved in any given year; conversely, a few years might pass with no good opportunities.
7. This magnitude of capturing and moving bears would result in approximately 3 to 6 bears being moved to the GYE per grizzly bear generation (see below). If one-half of the bears moved stayed in the Yellowstone, survived long enough to reproduce, and produced (or sired) a cub that survived to adulthood, approximately 1.5-3 effective migrants per generation would gradually be added to the Yellowstone population. (See below for additional information and justification).
8. If subsequent monitoring (see below) indicated the need for additional bears, additional trapping would be considered. If subsequent monitoring indicated greater fidelity and survival among augmented bears than anticipated, fewer might be moved.

9. All individuals translocated would be fitted with a GPS collar, micro-chipped, and tissues for DNA monitoring would be obtained. The IGBST (or cooperating staff) would track any translocated individuals as part of their routine telemetry monitoring program. Attempts would be made to continue monitoring females post-denning, to document presence of litters. We anticipate, however, that direct observation of offspring from augmentees will be difficult and incomplete. Thus, the genetic monitoring program that is currently in place would continue to document and quantify any reproductive contribution from translocated animals.
10. Translocated individuals would be considered experimental[1] animals, and either moved or euthanized should they cause conflicts with humans.
11. For any translocated individuals that survive and remain in the GYE Demographic Monitoring Area (DMA) at least 1 year, that year's allowable mortality limit for that gender for the GYE (as per the GYE Conservation Strategy) would be increased by one to account for the unanticipated addition of that individual, reinforcing that the augmentation is for genetic, not demographic purposes.
12. As per the NCDE Conservation Strategy, a bear removed from within the NCDE DMA would count against the NCDE's mortality limit (albeit could be accompanied by an asterisk to clarify that the bear might not have died, thus helping inform a potential programmatic review).

Required Permissions and Suggested Processes/Protocols

Permissions and approvals

1. While federally listed, USFWS approves all relocations and translocations of grizzly bears in the contiguous 48 states. With limited exceptions, grizzly bears have not previously been moved from one "ecosystem" to another. To expedite real-time decision making, an omnibus approval of this program from USFWS is part of this process.

2. Landowner approval. FWP only releases grizzly bears where the landowner has provided pre-approval. Although there is no particular reason to consider 'northern' grizzly bears differently from those coming from closer by, because this would be a new program, we would anticipate obtaining specific approval from landowners in the GYE (typically USFS) and affected states for releases of these bears.

3. Newly enacted legislation requires that, while federally listed, the Montana Fish and Wildlife Commission pre-approve sites for any grizzly bear releases that would occur within Montana. A list of 32 potential relocation sites in the GYE (anticipating possible relocations of conflict animals) was presented to the Commission for consideration on October 28, 2021 and approved for a five-year period on February 4, 2022.

4. FWP operates its grizzly bear conflict response program under annually renewed memoranda of agreement with the USFWS; thus, no new permits or addenda to these annual agreements would appear to be required.

Biological Considerations

[1] Not to be confused with the legal definition of an "experimental population" in ESA 10(j) sense.

Acknowledging at the outset that ‘biological’ considerations are not entirely separable from ‘social’ considerations (and that both are important), we categorize biological issues into four: 1) characteristics of a candidate bear, 2) where captured, 3) where released, and 4) when captured/released.

1) Characteristics of bears being considered (sex/age/history)

a) Management history: Bears with a history of involvement in bear-human conflict, even as offspring, will not be considered candidates for translocation. Furthermore, bears captured away from human settlements will be the best candidates to minimize the likelihood of post-release bear-human conflict.

b) Age/sex of bear: Knowledge of bear behavior and information about post-release movements help inform which sex and age categories are most likely to result in success. Younger bears, primarily between the ages of 2 and 5, often undergo natal dispersal whereby they move away from their natal home range to settle in their own permanent home range. In general, male bears are very likely to disperse, tend to disperse large distances, and can be highly transient for more than a year. In contrast, female bears are more likely to remain near their natal range, rarely disperse large distances, and are less transient than males. Nonetheless, occasional long-distance female dispersal does occur. This natural tendency for movement by young bears of both sexes, in the pursuit of finding and establishing their own permanent home range, is associated with less frequent homing and higher fidelity to release areas when they are translocated. Continued transiency and wide-ranging movements following translocation are not uncommon until bears settle in their permanent home range. In the Cabinet Mountain augmentation program, all of the translocated bears known to have successfully bred were translocated when they were within this age group: three females and one male were translocated as 2-year-olds and one male was translocated as a 4-year-old. Overall, both female and male bears in this age class are good candidates for translocation, as long as evidence indicates they have not previously reproduced. It is likely that eventual reproduction by females would be easier to document via direct observations, whereas male reproduction will be detected through genetic analysis. Successful female reproduction is constrained to litters every 3 years, but successful males have the potential, but certainly not the certainty, of breeding every year and fathering offspring with multiple females.

By the time bears reach the of 6 or 7 years, most have established a permanent home range and have become reproductively active. Consequently, when adult bears are translocated, they frequently return or attempt to return to their home range, even when moved distances >200 km and even when accompanied by offspring. Homing bears generally move in a linear fashion even though it may take them some time to determine the correct direction toward their home range. When translocated long distance, it is not unusual for bears to take more than a year to return home. Overall, reproductively active adult bears are not good candidates for translocation to augment the GYE population.

Cub and yearling bears are usually still dependent on their mother, however survival of orphaned or early-independent bears in these age classes has been observed. When translocated independently of their mother, initial movements of cub and yearling bears are usually more restricted than those of older bears, but they can also become more transient over time, consistent with their natural dispersal behaviors. They likely have a good probability of settling in the release area, however their survival is likely to be lower than older bears. Their survival and ability to settle in a home range is probably most compromised where the resident bear population density is high. Orphaned cub or yearling bears may be good candidates for translocation, as long as their body size and condition suggest good potential for survival on their own. Given that these bears are unlikely to reproduce for at least 4 years, recapture or genetic analyses would likely be required to document any eventual reproduction. There are no sex/age combinations that would automatically disqualify a bear from consideration. However, evidence and experience suggest that some are better choices than others given other considerations, and that each comes with unique sets of attributes:

i) **Sub-adult female (age ~ 2 to 5, as estimated in the field).** These bears are generally the strongest candidates because they are *relatively* likely to remain in the target area without conflict with humans. A 4-year old female would likely be among the easiest to monitor (collar longevity is good) for survival and reproduction. If later bred, her offspring would most likely be hybrids (sired by a GYE male, i.e., she'd be an effective genetic migrant), but even if pregnant when moved, she and any surviving offspring could mate with GYE in future years. Downsides are that it may require 1-3 years before she is mature enough to breed (particularly if younger). If younger (i.e., <4), collar retention could be problematic. However, younger NCDE sub-adults (aged 2-3) that were translocated > 4 times their sex-specific home range radiuses displayed slightly greater fidelity to areas in which they were released than females aged 4 or 5. If it is possible to capture the independent offspring of females known to be free of conflict (e.g., if collared for trend monitoring), such an animal would probably be unfamiliar with human-related attractants, and thus likely to remain conflict-free. Both managers and the public should be aware, however, that even bears in this optimal sex/age group may display homing movements, or wander considerably before settling down.

ii) **Sub-adult male (age ~2 to 5, as estimated in the field).** These bears are generally less suitable candidates than females of similar ages (above), because a) they are more likely than females to get into conflict situations, b) they are more likely than females of similar age to suffer mortality, even without an obvious human-conflict, c) they are more likely than females of similar age to become displaced by larger males, and thus possibly leave the GYE entirely, d) it may require some time before they can establish themselves as breeders if they are not displaced, and e) collar retention is not as good as among females. However, in the unlikely event that a subadult male can safely establish itself, it could breed at a younger age than a subadult female (have less time exposed to risk before it makes a genetic contribution). At least 2 male Cabinet augmentees are known to have later sired subs. Sub-adult males are an option if other considerations are strongly positive.

iii) **Orphaned cub of the year (either sex).** Although there is documentation that some orphaned cubs can survive without their mothers, our assessment is that the additional stress of putting them into a unique environment makes their survival unlikely. Orphaned cubs should not be considered candidates.

iv) **Orphaned yearling (either sex**). The likelihood of orphaned yearlings surviving and finding a new home in the GYE is probably higher than of orphaned cubs. Yearlings of a female that had a history of conflict would not be candidates due to the likelihood that they already learned unacceptable behavior. However, yearlings orphaned as a result of mortalities of non-conflict mothers could be considered candidates. If >1 yearling were captured and moved together, their survival would probably be higher than for a single animal and would also double the potential of ultimately producing an effective genetic migrant. However, yearlings would require more years (probably 4) before they could breed, and would be even more difficult to monitor long-term via telemetry than subadults.

v) **Adult female (age 5+, as estimated in the field).** An adult female unaccompanied by cubs in mid-summer has high likelihood of already being bred; thus, cubs she might produce overwinter in the GYE would not be genetically effective migrants (and would not constitute success). However, those cubs would carry NCDE genes, and thus any that survived to become breeders themselves would increase the pool of potential effective migrants. An adult female in mid-summer who'd lost a litter would be very likely to be bred by a GYE male the following spring, assuming she survives and stays in the target area that long. Adult females would offer the greatest opportunity for monitoring their genetic success, an important criterion because they are most amenable to long-term radio-monitoring, and can sometimes be observed visually (and if accompanied by cubs, reproduction documented). However, adult females generally are the most likely to exhibit homing movements (see above), and thus are poor candidates for this program.

vi) **Adult male (age 5+, as estimated in the field).** Although generally not considered an optimal choice due to concerns about potential human-bear conflicts and competition with resident adult males in the release area, there could occasionally be situations in which an adult male could be considered. An adult male that survived and avoided conflict could conceivably mate during the breeding season immediately following translocation, and if it became established, make a disproportionately large genetic contribution. A downside is that documenting effective migration of males would require long-term genetic data and not be assured; it is also difficult to keep collars on adult males. Consider if a) a translocation site can be found at which potential for conflict is low, and/or b) capture is very late in the season, such that the animal has already built up fat reserves and dens shortly after release. Late-season releases would be contraindicated where big-game hunting is still occurring.

2) Areas for capture

i) Although habitat similarity to the GYE (another consideration) could be greatest for an animal captured at the southeastern extent of the NCDE distribution (and such bears might appear to be "trying" to get to the GYE on their own), such an animal could have a higher likelihood of returning (i.e., not remaining within the target area).

ii) We take it as a given that habitat characteristics of the release site will differ from those at the capture site, and challenges translocated animals will face are factored into the expected probability of success. Although 'matching' habitat of the donor to recipient area would be ideal, it's not a critical consideration given how adaptable bears are. That said, bears living in the relatively mesic, huckleberry-dominated areas in the northwest portion of the NCDE are probably not the best candidates, at least initially. As well, potential candidate bears in this area are high priorities for the Cabinet augmentation program.

iv) A likely constraint for capture areas is the need to use culvert traps (so that bears can easily be moved from the site), and thus road access (unless culverts could be flown into remote locations).

v) A female bear originating in a Bear Management Unit (BMU) or Occupancy Unit (OU) where meeting occupancy standards has been a concern should not be a strong candidate.

vi) As with any grizzly bear capture operation, good communication and close coordination with local land managers is critical.

3) Release areas

At this point in the process, we consider areas at a coarse geographic scale. Specific release sites should be well-vetted, and offer the lowest possible opportunity for released bears to find trouble, while recognizing that bears generally don't stay in the immediate area where they are released. Appropriate sites would be within the GYE DMA, but not otherwise be constrained geographically at this coarse level of consideration. That said, bears released where a large expanse of relatively undeveloped landscape exists between the site and the bear's original home range are less likely to engage in conflict behavior or exhibit homing.

We seek areas with enough bears that translocated animals can find (or be found by) mates, but not such a high density that competition or aggression from resident bears will increase the chance of intraspecific predation or displacement outside the GYE DMA. If possible, local density estimates such as produced by Bjornlie et al. (2014) and IGBST (unpublished data) should be consulted, but qualitative assessments made by locally-based staff will be crucial as well. Expecting that translocated bears may not remain close to the release site, an important consideration is the spatial extent and configuration of habitat surrounding the release site where conflicts with humans are unlikely.

As with any grizzly bear translocation, good communication and close coordination with local land managers is critical.

i) **Yellowstone National Park**. Because livestock are absent and attractants generally well controlled, YNP should be strongly considered at the outset of this program. Challenges would be identifying areas where resident grizzly bears are not too dense (see above, e.g., not Hayden Valley), and where recreationists are not highly concentrated.

ii) **Wyoming, outside of YNP**. There may be areas, particularly in the northern portions of the BTNF, where attractants are rare or well-managed, and where a translocated bear would have a good chance to mate with other bears without coming into conflict. Potential areas include the southeastern portions of Blackrock, Togwotee Pass, and Moccasin Basin, where cattle allotments have been bought out or retired, but there is still gated road access to move a bear far from any developed areas (but not further south where cattle density increases).

iii) **Montana, outside of YNP.** Generally, areas where an augmentee might be released in the Montana portion of the GYE DMA are closer to humans (recreationists, livestock, homesites). Thus, we recommend gaining some experience with the program before considering sites in Montana.

iv) **Idaho, outside of YNP.** Not a candidate translocation recipient at this time.

iv) **Grand Teton National Park**. Not a candidate translocation recipient at this time.

4) Time of year

i) Biologists have typically considered it unwise to transport animals early after den emergence, as bears that time of year are particularly hungry, many plants-based food sources are not yet available, and livestock young are small and vulnerable. Snow typically reduces road access early in the bear-year, which in turn means that capture and release sites are likely closer to people. Spring black bear hunting can also constrain grizzly bear captures.

ii) July and August are typically considered the optimal months to translocate bears, as plant-based food sources are peaking and bears are not yet in hyperphagia. Eighteen of the 22 Cabinet augmentees were moved in July or August to match the peak of huckleberry production. However, the mast peak seen in the Cabinets does not characterize the GYE, so a somewhat earlier time window should be considered.

iii) September through mid-October are generally avoided because i) some bears in hyperphagia descend to low elevations where human attractants are common, and ii) of overlap with big-game hunting. The latter concern would be lower if released centrally within YNP.

iv) Although few data are available to inform it, the possibility that grizzly bears might be successfully translocated very late in the active year, just prior to expected denning, holds promise. Such a bear should have already fattened up, and even in an unfamiliar place we do not expect it to have difficulty finding a place to den. Upon emergence, it may then be more likely to consider its denning area a new home.

In summary, we recommend that for the first few years of this program, managers adopt a conservative approach, moving only bears that are most likely to stay in the GYE, survive, and breed; moved only during the optimum time of year; and released where success is most likely. With time and experience, criteria for acceptable candidate bears, source locations, release locations, and timing of movements can all be revisited if new information becomes available, and this protocol updated and revised if appropriate.

Other considerations

1. FWP and USFWS are cooperating on a long-term project to augment the Cabinet Mountains population; since 2005, all bears have come from FWP Region 1 (Flathead, Swan, Stillwater drainages). The objective is to move 2 subadult bears/year, although fewer have been moved in some years. GYE genetic augmentation would be a concurrent program but could transpire over a more relaxed time schedule. Ideally, appropriate bears can be found for both programs.

2. Bears removed (live) from the NCDE for augmentation are counted as "mortalities" following the NCDE Conservation Strategy when assessing whether thresholds have been exceeded. Typically, capture efforts for augmentation would occur before that year's total mortality has been documented; it's thus possible for mortalities occurring later in the year to put that year's total "over" the threshold. However, the threshold is calculated on a 6-year running average, and because the total reported and unreported estimate would be known for the previous 5 years, the likelihood of reaching the threshold because of live removals can be estimated (albeit with some uncertainty). Because this GYE augmentation is intended to produce 1 or 2 effective migrants per bear generation length (i.e., need not occur rapidly), it would be reasonable to hold off capture efforts in years in which removing more NCDE bears could cause the threshold to be exceeded.

3. Given considerations outlined in this document, we anticipate that trapping efforts for appropriate bears would be planned and deliberate or be associated with ongoing research and monitoring efforts. It is very unlikely that an appropriate bear would be captured in the course of conflict response work. Thus, additional resources will be required from donor agencies.

4. If released in Montana by MFWP (outside YNP) while bears are ESA-listed, the release site would have to be one previously approved by the Montana Fish and Wildlife Commission. This constraint would not apply if released by USFWS.

5. If released in Wyoming (outside a NP), WGFD must notify the county sheriff of the county in which the release takes place within 5 days, and issue a press release (W.S. 86 § 1).

6. Released bears will undergo standard data collection and processing, including collection of genetic samples, and must be PIT-tagged, ear-tagged, and outfitted with a GPS telemetry device.

DETAILED BIOLOIGCAL BACKGROUND

Grizzly bears living in the GYE have been isolated from other grizzly bear populations possibly for over 100 years, and thus the genetic effects of small population size raise concerns. No immigrants into the GYE population have been documented to date (Haroldson et al. 2010; M. Haroldson, USGS, pers. comm., 2021), and heterozygosity and allelic diversity are lower than most other North American grizzly bear populations for which data are available. However, these 2 metrics of genetic diversity declined very slowly if at all from 1985 to 2010. The rate of inbreeding has been very low since 1985, and no physiological, behavioral, or demographic effects indicative or associated with inbreeding have been detected. Importantly, estimates are that effective population size (the summary metric best suited to consider genetic effects) has increased over the estimates of 1910-1960, continued to increase during 1985-2007, and is well above the level where the short-term effects of reduced genetic diversity (i.e., inbreeding, genetic drift) would be expected.

Thus, all indications are that Yellowstone grizzly bears are genetically well-adapted to their existing environment and facing no immediate threat related to population genetics. However, the Yellowstone population is sufficiently small from a genetic perspective that isolation from other populations poses risks for its *long-term* viability (> 100 years). Although no genetic issues currently limit the ability of grizzly bears in Yellowstone to survive and reproduce normally, their ability to respond evolutionarily to unknown future environmental or other challenges may be limited by low allelic diversity combined with isolation. Thus, introduction of genetic material from other grizzly bear populations would reduce the long-term risks associated with loss of allelic diversity in the Yellowstone grizzly bear population.

Best estimates are that any long-term genetic risks can be ameliorated by the effective migration into Yellowstone of as few as 1 to 2 animals per generation (10-15 years) if continued indefinitely into the future. Thus, although connectivity is required over the long-term to alleviate risks, such genetic connectivity can be thought of as a slow and continuous trickle of bears rather than a sudden and dramatic increase of gene flow. Recent geographic expansions of GYE grizzly bears in a northwesterly direction, and of NCDE area grizzly bears in a southeasterly direction have increased the probability of natural genetic connectivity in the future. A major impediment to achieving connectivity is Interstate Highway 90, and in particular the rapidly increasing level of human development associated with the greater Bozeman area.

Why do we think that genetic augmentation is necessary, and why do we think the relatively few animals we suggest here will suffice? Consider the question “How many animals are enough to ensure long-term persistence” by focusing on minimizing the chance that erosion of genetic diversity within a small, isolated population will render it unable to evolve, if needed, to changed conditions in the future. We know that larger populations generally have more genetic diversity — more options available from which to develop adaptations to differing conditions — than smaller ones. But how large is large enough to maintain needed evolutionary potential? We don't have the luxury of observing a variety of wild populations subjected to changing conditions to see which ones successfully coped and which did not. Instead, we need to depend on theory, augmented by well-considered simulation models.

In 1980, geneticist Ian Franklin postulated that an effective population of 500 would be large enough to allow beneficial mutations to balance genetic erosion (in particular, "genetic drift") indefinitely, and was thus a useful rule of thumb for answering the question "How many are enough to retain the evolutionary potential to cope with future change" (Franklin 1980)? Since then, some scientific dispute about the "500 long-term rule" has emerged (Jamieson and Allendorf 2012, 2013; Frankham et al. 2013); FWP agrees with Jamieson and Allendorf (2013) that it retains usefulness in considering long-term needs for population size.

Importantly however, the 500 number refers to the "effective" size, not the number of animals. The effective population size (N_e) is defined as that which will lose genetic variability at the same rate as an "ideal" population[2]. Because in almost all wild populations, N_e is smaller than the actual (census) number of animals (N_c), more than 500 animals would be needed in order to satisfy Franklin's rule-of-thumb. What is the relationship between N_e and N_c in grizzly bears? In reviewing a number of equations relating these 2 quantities at the time, Harris and Allendorf (1989) created simulations of grizzly bear populations, and concluded that, based on demographics and breeding structure, N_e was likely to be in the range of $0.24N_c$ —$0.32N_c$, depending on assumptions used. This suggested that a grizzly bear population would need to number ~ 1,560 to 2,080 to meet Franklin's criterion. Since then, advances in genetics and theory have allowed better and more data-driven estimates of N_e for the GYE grizzly bear population. Kamath et al. (2015), estimated that the N_e/N_c ratio had, in recent years, been between 0.42 and 0.66 (suggesting between 760 and 1,190 bears needed to satisfy Franklin's rule of thumb). Regardless, the long-term need for occasional genetic interchange between geographically discrete grizzly populations has not seriously been questioned by biologists (and is not questioned by FWP).

A related question follows: if a population is isolated but capable of being reached by occasional migrants from another presumably larger and more genetically diverse population, how many migrants are needed to effectively link the two genetically, and how often must such immigrations occur, in order for the entire assemblage to both be genetically secure while retaining any adaptive divergence? Sewell Wright, one of the founders of modern conservation genetics, had proposed decades ago that, under a number of simplifying assumptions, a single migrant per generation would be sufficient to prevent loss of heterozygosity and allelic diversity within a vulnerable subpopulation while still allowing it to respond adaptively to local conditions (Wright 1931). This noteworthy result derives from fact that a single migrant would provide a relatively large infusion of genetic material to a small population, and although it would provide a proportionally smaller benefit to a larger population, the very fact of large size would reduce the need for the immigration. A number of simulation studies later confirmed that the one-migrant-per-generation (OMPG) rule-of-thumb maintained its validity under a variety of assumption violations typical of real-world populations (Mills and Allendorf 1996, Wang 2004), and thus that OMPG, or perhaps slightly more than one, remained a useful long-term goal. A genetic metric to reflect the balancing between assuring that the target population would maintain its evolutionary potential while

[2] Defined as one with discrete, non-overlapping generations, that doesn't vary in size annually, and in which the contributions of each member to the succeeding generation are randomly distributed (i.e., described by a Poisson distribution).

still maintaining necessary local adaptations is called F_{ST}, which under OMPG would, after a sufficient number of years, equilibrate at 0.2

Of course, a “migrant” in this sense is not merely an animal that travels from one population to another. For it to perform as the OMPG theory predicts, the migrating animal must contribute to the gene pool after arriving, i.e., breed with a resident. Put another way, the ‘M’ in OMPG must be an “effective migrant”. What about the ‘G’ in OMPG? How long is a generation for grizzly bears? Using similar methods to those used to estimate N_e for Yellowstone grizzly bears, Kamath et al. (2015) estimated it at about 14 years. To date, we have no evidence that any migrants, effective or otherwise, have made it from the NCDE to GYE area populations.

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