

Yellowstone Bison—Should We Preserve Artificial Population Substructure or Rely on Ecological Processes?

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Halbert et al. (2012) analyzed microsatellite genotypes collected from 661 Yellowstone bison sampled during winters from 1999 to 2003 and identified 2 genetically distinct subpopulations (central, northern) based on genotypic diversity and allelic distributions. On the basis of these findings, they raised concerns about the management and long-term conservation of Yellowstone bison because of disproportionate culling of the 2 subpopulations in some winters. The data and findings of Halbert et al. (2012) are significant and useful for managers charged with conserving these iconic wildlife. However, their article provides information regarding the behavior and management of Yellowstone bison that does not accurately portray historic or current conditions. This response clarifies those conditions and challenges some of their apparent deductions and recommendations.

Halbert et al. (2012, p. 1) indicate that Yellowstone bison provide an opportunity to examine a “. . . natural population substructure, which could have important implications for the long-term evolution of these populations.” They assume “. . . the Yellowstone population was not subdivided before 1936” and that “these 2 subpopulations [central, northern] have differentiated in a relatively short period of approximately 8 generations [64 years]” (Halbert et al. 2012, p. 5, 7). However, these statements ignore that humans contributed to the observed population and genetic substructure in Yellowstone bison by nearly extirpating them in the late 19th century (except for approximately 23 bison that survived in central Yellowstone) and then by creating another breeding herd in northern Yellowstone at the turn of the 20th century from 21 bison of unrelated breeding descent and divergent genetic stock that were relocated from northern Montana and Texas (Meagher 1973). A few individuals from the endemic central herd were introduced into the northern herd in the early 1900s, whereas 71 bison from the northern herd were relocated to central Yellowstone during 1935–1936 (Cahalane 1944). The northern herd was not

released from traditional livestock management practices and allowed to evolve natural patterns of distribution until the 1950s—which likely contributed to some geographic separation between the herds (Meagher 1973). Further, each herd was sporadically culled from the 1950s to present (Meagher 1973, White et al. 2011b). Thus, the history of Yellowstone bison suggests the population substructure and genetic differentiation was substantially influenced by a human-induced bottleneck in the late 1800s and the effects of human stewardship thereafter. As a result, there is evidence that the existing genetic substructure was artificially created.

Halbert et al. (2012, p. 2,5) state that “Radiotelemetry data indicate the [central and northern] herds remain isolated during the summer breeding season” and “the number of migrants into and out of each subpopulation each generation is about 2 ($N_m = 2.3$) or approximately 1 every fourth year.” This statement and estimate may generally reflect conditions during the period of intense human stewardship (1900–1968) and subsequent increase in bison abundance and distribution during the period of ecological process management (Plumb et al. 2009). However, extensive monitoring of the movements and productivity of radio-collared bison since 2005, when the population reached an abundance of approximately 5000 bison, suggests that emigration and gene flow is now much higher. Since 2007 (one half of one generation), biologists have detected 17 radio-collared bison emigrating between the central and northern herds and remaining through one or more breeding seasons (see Supplementary Table 1 online). Female bison rarely travel alone, so dispersal by these marked females likely represents emigration in groups of 25–40 bison each time, which increases the probability that gene flow occurred. Eleven of these 17 radio-collared bison produced calves on their new range (e.g., northern) that were conceived on the range they left (e.g., central). At least 23 calves were produced by these dispersing bison through mating and calving on their new

range. These observations of female emigration and subsequent reproduction on a new breeding range are supported by low F_{ST} estimates derived from microsatellite genotypes collected from 152 feces of Yellowstone bison sampled during breeding seasons between 2006 and 2008 (Gardipee 2007; G. Luikart, unpublished data). The low F_{ST} estimates suggest that there are approximately 10–20 emigrants per generation (see Supplementary Table 2 online). The natural process of emigration by bison was likely facilitated by the pioneering behaviors of animals responding to higher abundance (density) and deep snow conditions that limit forage availability and foraging efficiency (Gates et al. 2005). Some biologists suggest these increased movements of bison between the central and northern herds during winter reflect the effects of packing snow-covered roads to facilitate over-snow vehicle recreation during winter. However, grooming has occurred since the 1970s and scientific findings suggest that bison use of travel corridors that include these groomed road segments would persist whether or not roads were groomed (White et al. 2009). Regardless, recent observations of gene flow between the central and northern breeding herds are substantially higher than previous estimates.

Halbert et al. (2012, p. 9) deduce that “. . . the identification of genetic subpopulations in this study raises serious concerns for the management and long-term conservation of Yellowstone bison” which “. . . have long been treated as a single metapopulation whereby the total number of bison is assumed to be the most important factor in determining appropriate winter cull levels.” It is correct that the Interagency Bison Management Plan (USDI and USDA 2000) provides guidelines for managing toward an end-of-winter abundance for the entire population around 3000 bison. However, management plans and monitoring/research to inform and adjust actions, including culling activities, have considered the two breeding herds (Angliss 2003, Clarke et al. 2005, Gates et al. 2005, Gardipee 2007, Fuller et al. 2009, Geremia et al. 2012). Although the 2 subpopulations have been disproportionately culled in some years, biologists have clearly warned of possible demographic effects if large culls were continued over time (White et al. 2011b). Biologists have also acknowledged that it is not clear how large-scale culling might influence the genotype diversity and allelic distributions of the subpopulations over time (White et al. 2011b). These analyses and uncertainties led to the implementation of several adaptive management adjustments to the Interagency Bison Management Plan designed to minimize future large-scale culls of bison, evaluate how the genetic integrity of bison may be affected by management removals (all sources combined), and assess the genetic diversity necessary to maintain a robust, wild, free-ranging population that is able to adapt to future conditions (USDI et al. 2008). In addition, the National Park Service developed a rigorous monitoring plan for Yellowstone bison that characterizes the bison inhabiting Yellowstone as a single population with significant substructure and includes randomly sampling bison from primary breeding locations during July and August to identify genetic subdivisions and estimate gene flow within the Yellowstone population (White et al. 2011a). The plan acknowledges it will be necessary to

sample bison across decades to determine if existing subpopulations are converging or becoming more divergent and whether management actions are having a significant influence on population substructure. Furthermore, each winter biologists use telemetry, ground observations, and aerial distribution surveys to track movements of bison and attempt to differentiate animals from each breeding herd when they approach the boundary of the park and become subject to management actions. This approach does not provide absolute certainty with respect to breeding herd membership, but has been relatively effective at allowing managers to monitor movements by bison and estimate the proportion of culls from each breeding herd. Thus, total population abundance is not the only primary factor considered in determining management actions for Yellowstone bison. As an example, the management plan for Yellowstone bison during winter 2012 clearly indicates a desire to progress toward approximately equal numbers of bison in each breeding herd and selectively cull bison from the northern herd (which is currently larger), while minimizing removals from the central herd (Geremia et al. 2012).

Halbert et al. (2012:9) conclude that “these observations warrant serious reconsideration of current management practices. The continued practice of culling bison without regard to possible subpopulation structure has the potentially negative long-term consequences of reducing genetic diversity and permanently changing the genetic constitution within subpopulations and across the Yellowstone metapopulation.” The authors further suggest that current management will “. . . erode the genetic distinctiveness between the 2 groups” (Halbert et al. 2012, p. 9). We agree that bison removals should be carefully managed to prevent unintended consequences and have referenced documents in this response that indicate such management is occurring with frequent assessments of progress toward desired conditions. However, we question whether the National Park Service should actively manage to preserve the genetic distinctiveness of each herd because history indicates humans likely facilitated the creation and maintenance of this population substructure. Rather, we recommend that the National Park Service continue to allow ecological processes such as natural selection, migration, and dispersal to prevail and influence how population and genetic substructure is maintained in the future rather than actively managing to perpetuate an artificially created substructure. The existing population and genetic substructure may be sustained over time through natural selection or it may not. Regardless, we submit that it is the conservation of the ecological processes that is important, not the preservation of a population or genetic substructure that may or may not have been created and/or facilitated by humans.

Yellowstone bison are a valuable conservation population because they represent the largest wild population of plains bison and are one of only a few populations to continuously occupy portions of their current distribution and show no evidence of hybridization with cattle in their genomic ancestry (Meagher 1973, Halbert and Derr 2007). Perhaps more importantly, Yellowstone bison are part of an intact predator–prey–scavenger community and move, migrate, and

disperse across a vast, heterogeneous landscape where the expression of their genes is subject to a full suite of natural selection factors including competition (for food, space, and mates), disease, predation, and substantial environmental variability. As a result, Yellowstone bison likely have unique adaptive capabilities compared to most bison populations across North America that are managed like livestock in fenced pastures with forced seasonal movements among pastures, few predators, selective culling for age and sex classifications that facilitate easier management (e.g., fewer adult bulls), and selection for the retention of rare alleles—the importance of which has not been identified. Modern society has placed restraints on wild bison distribution and, therefore, has an overarching influence on which evolutionary processes will be allowed to persist for this species. Given existing habitat loss and social concerns across the continent, it is unlikely that many additional populations will be allowed to increase in abundance and move across the landscape at a scale similar to Yellowstone bison (Boyd 2003). Thus, a few bison populations in the greater Yellowstone ecosystem (Jackson, Yellowstone), Canada (Pink Mountain, Prince Albert), the Henry Mountains of Utah and, potentially, Badlands and Wind Cave National Parks in South Dakota assume great importance and managers should be promoting the conservation of wildness and natural selection to retain adaptive capabilities, rather than preconceived notions of “natural” genetic or population substructures that were likely created or exacerbated by human actions.

Supplementary Material

Supplementary material can be found at <http://www.jhered.oxfordjournals.org/>.

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