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High genetic diversity can contribute to extinction in small populations

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Abstract

Human-driven habitat fragmentation and loss has led to a proliferation of small and isolated plant and animal populations that may be threatened with extinction by genetic factors. The prevailing approach for managing these populations is to maintain high genetic diversity, which is often equated with fitness. Increasingly, this is being done using genetic rescue, where individuals from populations with high genetic diversity are translocated to small populations with high levels of inbreeding. However, the potentially negative consequences of this approach have recently been highlighted by the demise of the gray wolf population on Isle Royale, which only briefly recovered after genetic rescue by a migrant from the large mainland wolf population and then declined to the brink of extinction. Here, we use ecologically-motivated population genetic simulations to show that extinction risk in small populations is often increased by maximizing genetic diversity but is consistently decreased by minimizing deleterious variation. Surprisingly, we find that small populations that are founded or rescued by individuals from large populations with high genetic diversity have an elevated risk of extinction due to the high levels of recessive deleterious variation harbored by large populations. By contrast, we show that genetic rescue or founding from small or moderate-sized populations leads to decreased extinction risk due to greater purging of strongly deleterious variants. Our findings challenge the traditional conservation paradigm that focuses on genetic diversity in assessing extinction risk in favor of a new view that emphasizes minimizing deleterious variation. These insights have immediate implications for managing small and isolated populations in the increasingly fragmented landscape of the Anthropocene.

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Main text

The prevailing paradigm in conservation biology prioritizes the maintenance of high genetic diversity in small populations threatened with extinction (*1–3*). Under this paradigm, genetic diversity is considered the primary determinant of fitness (*4*, *5*), and the negative effects of inbreeding are thought to be minimized by maintaining high genetic diversity. However, this paradigm is challenged by the observation that some species, such as the Channel island fox, can persist at small population size with extremely low genetic diversity and show no signs of inbreeding depression (*6*, *7*). This and other examples suggest that, rather than being mediated by high genetic diversity, persistence for small populations may instead be enabled by the purging of strongly deleterious variants, even when weakly deleterious variants increase in frequency (*6–10*). In this study, we investigate the genetic factors mediating the persistence or demise of small populations using population genetic simulations and demonstrate the counterintuitive and potentially detrimental effects of high genetic diversity in small and isolated populations. We argue that, in cases where populations are destined to remain small and isolated, management strategies should aim to minimize deleterious variation rather than maximize genetic diversity.

The motivating example for these simulations is the gray wolf population on Isle Royale, an island in Lake Superior that has long served as a natural laboratory in ecology and conservation biology (*11–14*). Following 70 years of isolation at a population size of ~25, the population was driven nearly to extinction by severe inbreeding depression, with just two individuals remaining in 2018 (*14*, *15*)(Fig. 1A). Recent findings have suggested that the collapse of the population was probably driven by the expression of recessive strongly deleterious alleles, which are present in the mainland wolf population primarily in the heterozygous state, but were driven to near-fixation in the island population after a mainland migrant 'genetically rescued' the population by producing 34 offspring (Fig. 1A)(*14–17*). In response to the decline of the wolf population, the US National Parks Service recently translocated 15 wolves to Isle Royale, which were drawn from three nearby large source populations with the aim of maximizing the genetic diversity of the new island population (Fig. 1B). However, the large ancestral population size of

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these migrants implies that they likely carry high levels of recessive strongly deleterious variation, potentially repeating the scenario that led to the initial population collapse. An alternative approach for genetic rescue or reintroduction initiatives might instead target historically smaller source populations with a history of purging of strongly deleterious variants, or screen populations for individuals with low levels of strongly deleterious variation. This approach could potentially alleviate problems with inbreeding depression by reducing the number of strongly deleterious alleles in the small, isolated population. Given the growing interest in genetic rescue as a management tool (*8*, *18*, *19*), such an approach could potentially have wide-ranging implications for conservation.

The applicability of population genetic models to understanding extinction has historically been limited by unrealistic assumptions that often ignore stochastic ecological factors and typically do not consider both weakly and strongly deleterious variation (*20*–*22*). Here, we use a novel population genetic simulation framework that combines ecologically-motivated models of population dynamics with realistic genomic parameters (*23*)(SI) to assess how demographic history, genetic diversity, and deleterious variation influence extinction risk in small populations. Our simulations aim to capture the ecological factors that may contribute to extinction in small populations, such as those observed in the Isle Royale population, by incorporating the effects of demographic and environmental stochasticity, and natural catastrophes (SI). Coupled with these stochastic population dynamics, we model a genome with parameters reflecting that of a canine exome, including 20,000 genes and 38 chromosomes that accumulate neutral and recessive deleterious mutations (SI). Using this framework, we first explore the effect of the ancestral population size ($K_{ancestral}$ = {1,000, 5,000, 10,000, 15,000}) on time to extinction following a population contraction or founding event (K_{modern} = {25, 50, 100}) (Fig. 2A). Although these parameter settings are motivated by the Isle Royale wolf population, they also mirror those of many other classic examples of inbreeding depression and genetic rescue, such as the Florida panther (*24*) and bighorn sheep (*25*).

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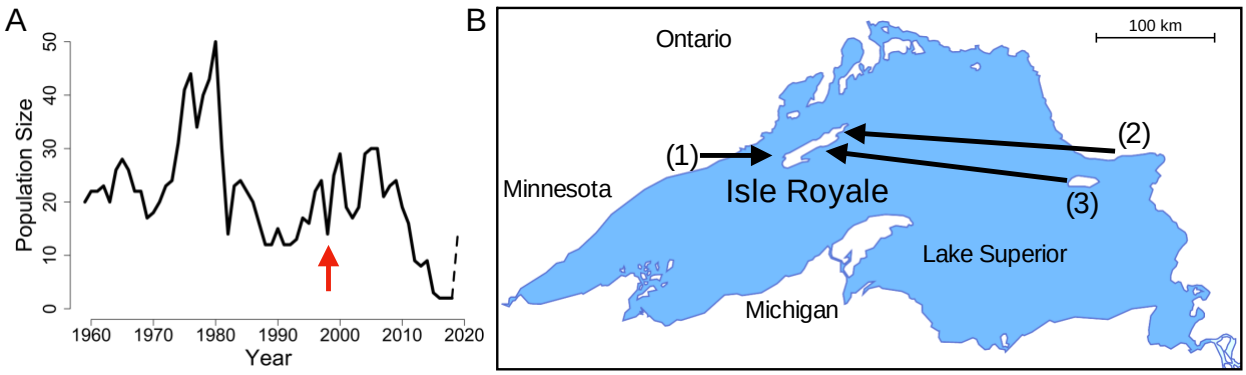

Figure 1: Isle Royale wolves. (A) Population trajectory of the Isle Royale wolf population since 1960. Red arrow denotes arrival of male migrant from mainland. Dashed line indicates population increase following translocation of 15 wolves in 2018-2019. (B) Map of Lake Superior showing locations of three source populations for translocation in 2018-2019. Source population localities include: (1) Grand Portage Indian Reservation (2 individuals), (2) Wawa, Ontario (3 individuals), (3) Michipicoten Island (8 individuals).

Our simulations demonstrate that large populations have higher levels of heterozygosity, as expected (Fig. 2B), as well as a greater number of strongly deleterious alleles ($s < -0.01$) per individual (Fig. 2C). Consequently, we observe a strong effect of ancestral population size on time to extinction following a population contraction (Fig. 2D), with populations that were historically large experiencing more rapid extinction. For example, given a modern carrying capacity of 25, a population with an ancestral carrying capacity of 1,000 will go extinct on average in 380 generations, whereas a population with an ancestral carrying capacity of 15,000 will go extinct in an average of 50 generations (Fig. 2B). This finding may be counterintuitive given the prevailing view that small populations should be less fit due to an accumulation of weakly deleterious alleles (*21*, *26*, *27*). The key driver of extinction that our simulations reveal is that larger ancestral populations carry more recessive strongly deleterious alleles in the heterozygous state (Fig. 2C). When the population contracts, elevated inbreeding exposes these recessive deleterious variants as homozygotes, leading to a reduction in fitness and driving extinction. The importance of recessive deleterious mutations in these simulations is further supported by the absence of this effect of the ancestral population size when mutations are assumed to have additive effects on fitness (Fig. S1-S2).

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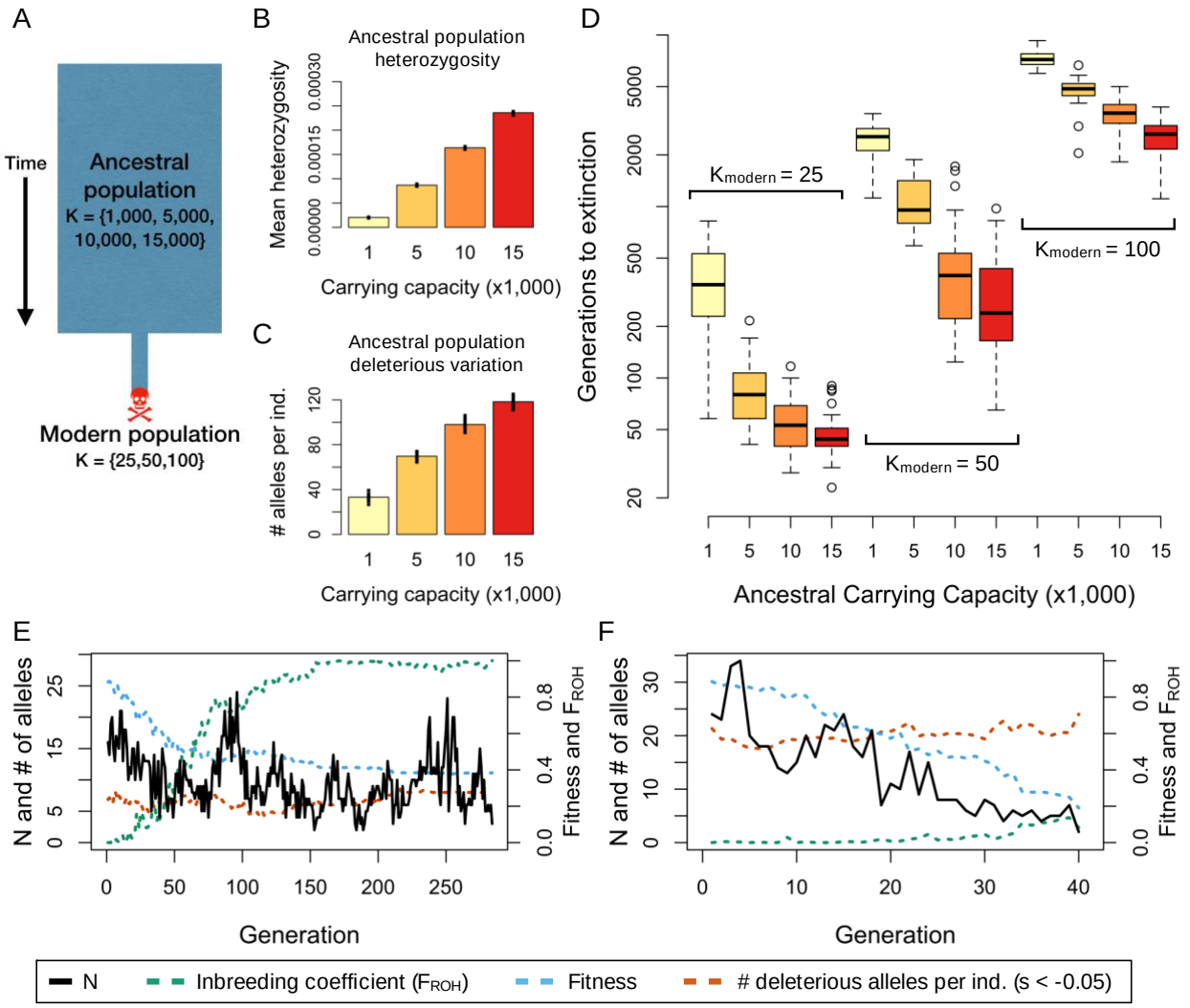

Figure 2: Ancestral population size impacts the time to extinction of small populations. (A) Schematic of the demography used in the simulations. (B) Mean heterozygosity of ancestral populations prior to contraction. (C) Average number of strongly deleterious alleles (s < -0.01) per individual in the ancestral populations prior to contraction. (D) Time to extinction for different combinations of ancestral and modern carrying capacities. Note that the y-axis is on a log-scale. (E) Representative population trajectory following contraction to a modern carrying capacity of 25 from an ancestral carrying capacity of 1,000 and (F) an ancestral carrying capacity of 15,000.

Examining individual simulation replicates provides insight into the dynamics of extinction in these populations (Fig. 2, E and F, Figs. S3-S5). Replicates with an ancestral carrying capacity of 1,000 contain few strongly deleterious recessive variants after the contraction to a carrying capacity of 25, translating to a less severe loss of fitness as the population becomes inbred and longer persistence (Fig. 2E). By contrast, replicates with an ancestral carrying capacity of 15,000 maintain high levels of strongly deleterious variation following contraction, leading to severe inbreeding depression and more rapid extinction (Fig. 2E). Even for replicates with identical

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parameter conditions, we observe a high degree of variability in time to extinction, which emerges from the interaction between the several forms of stochasticity in our model. For example, populations that by chance have a low carrying capacity due to environmental stochasticity immediately following the contraction quickly lose fitness due to inbreeding and are often unable to recover, even after the carrying capacity subsequently increases. However, populations that by chance had larger carrying capacities soon after contraction were better able to purge their strongly deleterious variants, leading to longer persistence. The trajectory of our simulated populations with an ancestral carrying capacity of 15,000 and modern carrying capacity of 25 (Fig. 2F, Fig. S3) closely mirror that of the Isle Royale wolf population (Fig. 1A), confirming that our simulations capture the genetic and ecological mechanisms relevant to the decline of the population.

Our simulations also demonstrate the importance of the carrying capacity of small, isolated populations as determinant of extinction risk (Fig. 2D). Smaller populations tend to go extinct most rapidly following a contraction, as expected given the higher levels of inbreeding in these populations as well as magnified effects of ecological stochasticity (Fig. S6). Nevertheless, the strong influence of the ancestral size was observed regardless of the post-contraction carrying capacity, highlighting the importance of both recent and ancestral demography in determining risk of extinction due to inbreeding depression.

We next examined how the levels of strongly deleterious variation and genetic diversity of the source population influence the effectiveness of genetic rescue, defined here as the magnitude of the increase in time to extinction. For these simulations, we fixed the ancestral carrying capacity to 10,000 and modern carrying capacity to 25 and split off source populations from the ancestral population prior to genetic rescue (Fig. 3A). We conducted genetic rescue after the recipient population decreased in size to five or fewer individuals by translocating five randomly-selected individuals from one of the following source populations: 1) a large source population remaining at the ancestral size (K=10,000); 2) a moderate-sized source population with long-term isolation (K=1,000 for 1,000 generations); 3) a small source population with

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relatively recent isolation (K=100 for 100 generations); and 4) a very small source population with very recent isolation (K=25 for 10 generations). These populations are highly variable in their levels of genetic diversity and deleterious variation (Fig. S7), providing a range of parameters to test how these factors influence the efficacy of genetic rescue.

Our results demonstrate that time to extinction following genetic rescue is highly dependent on the source population demography and levels of strongly deleterious variation (Fig. 3, B and C). For example, whereas genetic rescue from the moderate-sized source population (K=1,000) led to a dramatic increase in mean time to extinction relative to the non-rescue scenario of 162%, rescue from a large source population (K=10,000) resulted in a more modest increase of 28% (Fig. 3B). Genetic rescue from small and moderately-inbred populations (Fig. S8) also resulted in increases in mean time to extinction that exceeded that of the large source population (47% increase for K=100, 34% increase for K=25) (Fig. 3B). Although conventional thinking would suggest that the higher fitness of these larger populations (Fig. S8) would make them better able to rescue a population (*18*, *28*), individuals from these large populations carry many heterozygous recessive deleterious mutations that quickly become homozygous in the recipient population, resulting in more severe inbreeding depression. Indeed, these differences in time to extinction following genetic rescue are predicted by the average number of strongly deleterious alleles per individual in the source population (Fig. 3C), though not by source population average genome-wide heterozygosity (Fig. 3D).

The finding that source population deleterious variation predicts the efficacy of genetic rescue suggests that it may be possible to use genomic data to select individuals with low levels of deleterious variation to use for genetic rescue. We explored this strategy by selecting the individuals with the smallest number of strongly deleterious alleles ($s < -0.01$) from the large source population (K=10,000) for rescue. This approach resulted in an increase in mean time to extinction of 100% compared to the non-rescue scenario, a 57% increase relative to randomly selecting individuals from the large source population (Fig. 3B). By contrast, when we selected individuals with the highest genome-wide heterozygosity, we observed only a modest increase

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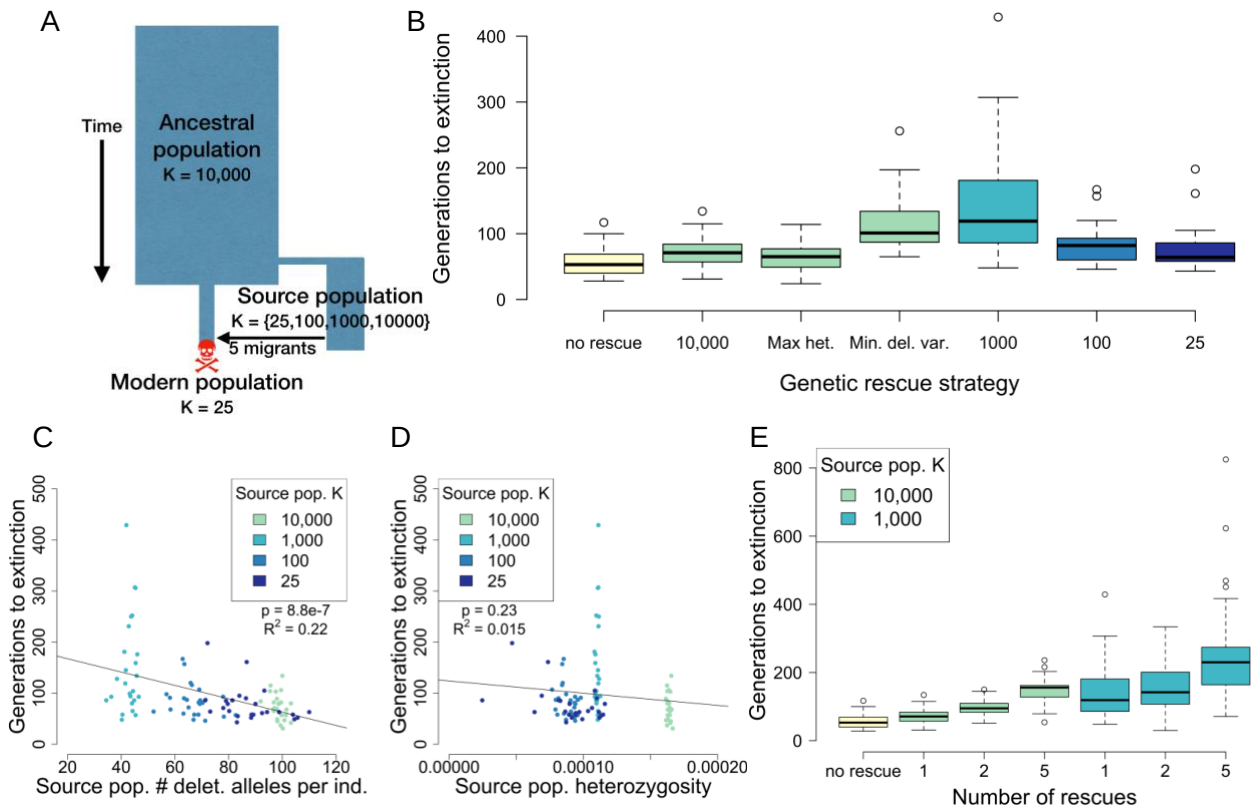

Figure 3: Source population deleterious variation determines the effectiveness of genetic rescue. (A) Schematic of the demography used in the simulation. (B) Time to extinction under different genetic rescue strategies. Numbers on x-axis denote source population carrying capacity; individuals selected with maximum heterozygosity or minimum number of strongly deleterious alleles (s < -0.01) were taken from K=10,000 source population. (C) Time to extinction following genetic rescue is negatively correlated with the number of strongly deleterious alleles (s < -0.01) per individual used for rescue. (D) Time to extinction following genetic rescue is not correlated with the heterozygosity of the source population. (E) Time to extinction as a function of the number of rescues from a large or moderate-sized source populations.

in time to extinction beyond the non-rescue scenario of 16%, a 10% decrease relative to selecting individuals at random (Fig. 3B). This result strikingly shows the potentially negative effects of trying to maximize genetic diversity in small populations, and highlights the role that genomic tools may be able to play in selecting individuals with low levels of deleterious variation for genetic rescue (*29*).

Lastly, we explored the effects of varying the number of migrants (1, 5, or 10) as well as the number of genetic rescue events (1, 2, or 5). These simulations show an approximately linear increase in time to extinction with increasing number of genetic rescues (Fig. 3E), suggesting that the efficacy of genetic rescue does not decrease with each additional rescue. However, we

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observed minimal effects of the number of migrants, implying that only a few migrants may be needed to achieve the beneficial effects of genetic rescue (Fig. S9).

Altogether, our simulations demonstrate the central importance of ancestral demography and strongly deleterious variation in determining the risk of extinction due to inbreeding depression in small and isolated populations. All else being equal, we find that populations that were historically large have a much higher risk of extinction following a population contraction compared to historically-smaller populations (Fig. 2D). These differences are mediated by the higher degree of purging of strongly deleterious variants in populations of small or moderate size (*6*, *8–10*, *26*). At first glance, this result may appear to be at odds with the thinking that individuals from larger populations should be more fit due to stronger purifying selection against weakly deleterious mutations (*4*, *21*, *26*, *27*). The dynamics of extinction that our simulations reveal is that, although large populations may have higher fitness, they also harbor higher levels of heterozygous recessive strongly deleterious variation (Fig. 2, B and C). The exposure of these strongly deleterious variants as homozygous in small populations can lead to dramatic reductions in fitness and drive rapid extinction, well before 'mutational meltdown' due to weakly deleterious variants can occur (*21*). By demonstrating that population contractions can result in levels of inbreeding severe enough to expose recessive strongly deleterious mutations and that this effect is sufficient to decrease fitness and ultimately lead to extinction, our simulations provide support for inbreeding depression being driven primarily by recessive deleterious mutations rather than overdominance (*8*, *30*). Although we did not model overdominance in our simulations, empirical evidence overdominance as a driver of inbreeding depression remains scarce, whereas recessive deleterious mutations are ubiquitous in diploid outbreeding organisms (*8*, *30*).

The influence of ancestral demography on extinction risk that our simulations reveal has wide-ranging implications for assessing the threat of extinction due to inbreeding depression in natural populations. Quantifying inbreeding depression in natural populations and predicting the threat it poses to extinction represents one of the major challenges for conservation

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biology, and it often remains unknown why some small populations appear to suffer from inbreeding depression and others do not (*8*). Our simulations demonstrate that these differences may be determined by the ancestral demography of a species. Consequently, we suggest that information on ancestral demography, which is increasingly becoming accessible using genomic data (*31*), could be more widely incorporated into extinction risk predictions. However, our simulations also reveal that the fate of small populations is highly stochastic, and that even under the same ecological and genetic parameters, time to extinction can vary substantially (Fig. 2D). This result can help explain the observation that some populations can persist at small size whereas others cannot, which may simply emerge from the stochasticity inherent in the eco-evolutionary process.

Our simulations have especially important implications for choosing source populations and individuals for genetic rescue or reintroduction, which are becoming increasingly important tools for maintaining small and isolated populations under growing anthropogenic pressures (*8*, *18*, *19*). Our results demonstrate that the effectiveness of genetic rescue can be greatly increased by targeting moderate-sized source populations with low levels of strongly deleterious variation (Fig. 3, B and C), in contrast to existing recommendations to target populations or individuals with high genetic diversity (*18*, *28*). Strikingly, we found that genetic rescue from large source populations with high genetic diversity was the least effective strategy, even when compared to rescue from small and moderately-inbred populations, and that targeting individuals with high genome-wide heterozygosity may in fact decrease the effectiveness of genetic rescue (Fig. 3, B and D). However, our simulations also show that genetic rescue from large source populations can be effective if individuals are screened for low levels of strongly deleterious variation (Fig. 3B). Furthermore, we demonstrate that the beneficial effects of genetic rescue may persist after multiple rounds of rescue (Fig. 3E), suggesting that repeated genetic rescue may be a viable approach when there are no other alternatives. Although much of the existing research on selecting source populations for genetic rescue has focused on the issue of outbreeding depression (*17*, *18*), we did not model this in our simulations due to the strong assumptions that would be required on the genetic basis of

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local adaptation (*30*). Moreover, an increasing number of studies have concluded that the risk of outbreeding depression is probably quite low (*18*, *19*, *28*, *33*), suggesting that it may be a less important consideration than deleterious variation.

Taken together, our results paint a bleak picture for the future of the Isle Royale wolf population, despite recent efforts to repopulate the island. Given the large ancestral wolf population size and small carrying capacity of Isle Royale, extinction due to inbreeding depression appears to be an inevitable outcome for any wolf population on the island (*14*, *15*). However, our results imply that the threat of extinction of the Isle Royale wolves and other small and isolated populations might be substantially decreased if management strategies are implemented that prioritize the minimization of deleterious variation. Rather than selecting source populations with the goal of maximizing genetic diversity, future translocation initiatives might instead target moderate-sized populations with a history of purging or screen large populations for individuals with low levels of deleterious variation. Given the great expense of most translocation programs, incorporating genomic tools represents a sound investment with the potential to substantially postpone the need for future intervention.

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