Grant Bruninga

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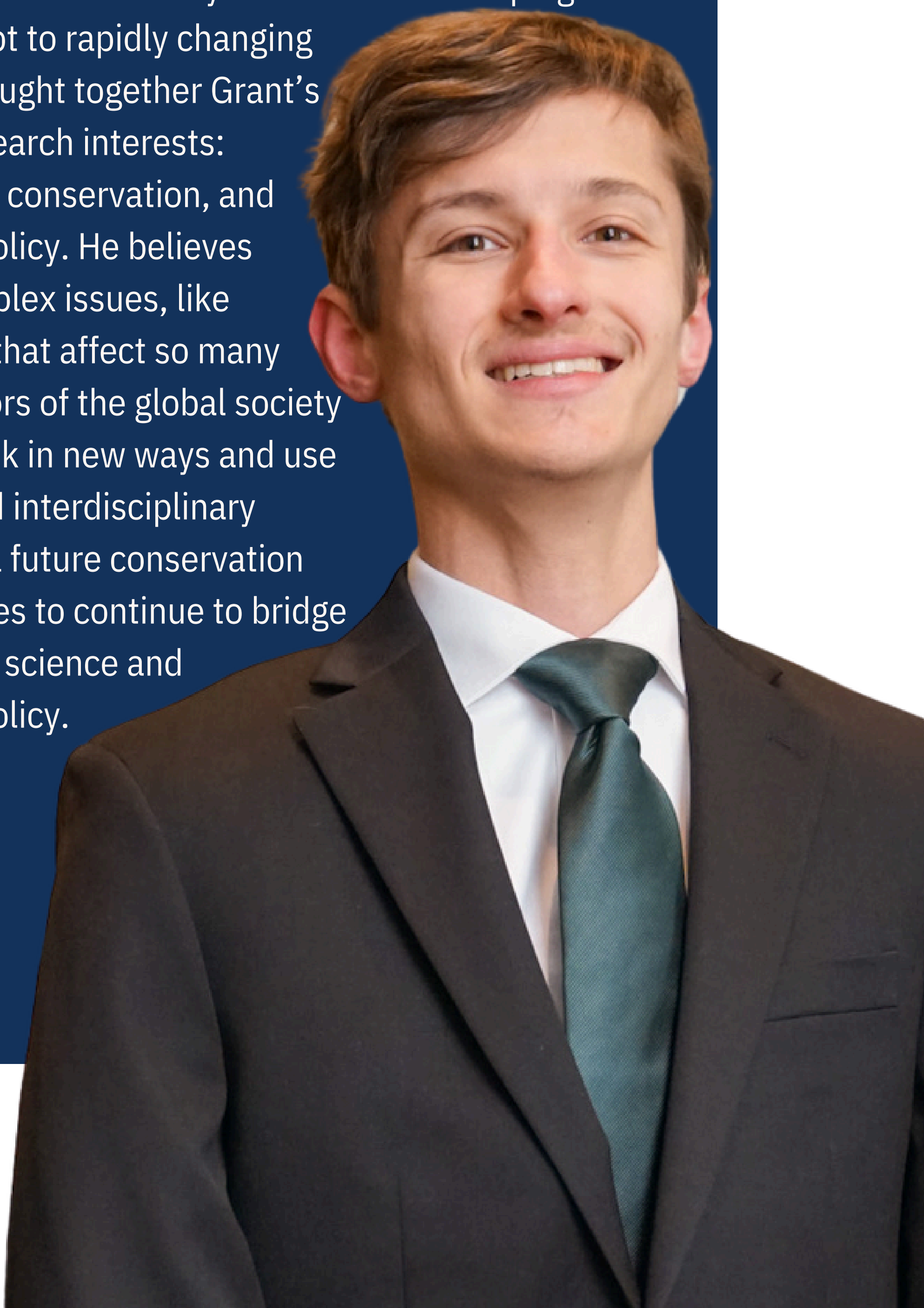
Investigating the role of hybridization in helping ecosystems adapt to rapidly changing environments bought together Grant's three driving research interests: genetics, wildlife conservation, and environmental policy. He believes that solving complex issues, like climate change, that affect so many people and sectors of the global society require us to think in new ways and use collaborative and interdisciplinary approaches. As a future conservation scientist, he hopes to continue to bridge the gap between science and environmental policy.



Hybridizing Hope: Hybridization as a Viable Method to Combat Mass Extinction in a Dynamic Environment

Grant Bruninga[1,*]

1 College of Natural Science, Michigan State University, East Lansing, Michigan, United States

* bruninga@msu.edu

Abstract

Historically, conservation managers and policymakers disregarded the hybridization of endangered species within their species (intraspecific) or between different species (interspecific) as a viable conservation strategy. Many believed that both processes produced non-viable offspring and decreased the fitness or ability of local populations of the target species to survive, a process called outbreeding depression. However, in an era of rapid climate change, hybridization confers vital genetic diversity and subsequent adaptive potential to populations who are struggling from inbreeding depression (or the loss of genetic diversity and fixation of deleterious mutations due to interrelated mating). This paper centers around the debate of whether hybridization should be prevented to preserve the adaptations in local populations or encouraged to preserve the ecological niche of the target species using scientific journal articles published between the years 2007 and 2023. This paper presents the debate over whether hybridization should be prevented to preserve local adaptations or encouraged to maintain the ecological niche of the target species, drawing on literature from the past two decades. Recent genetic studies from various species on intraspecific and interspecific hybridization events have shown that the effects of outbreeding may be significantly less detrimental than previously thought. Therefore, hybridization, if monitored correctly with recent advances in genetic and genomic technologies, could be used to maximize the survival of threatened species as their ranges continue to shift due to the onset of global climate change.

Introduction

Anthropogenic, or human-induced, impacts on the environment have resulted in the acceleration of habitat degradation, fragmentation, and destruction. Many species around the world are unable to adapt to the worsening of climatic extremes, with extinction rates reported to be between 100 and 1000 times greater than predicted pre-human background levels (De Vos et al. 2015).

Decreases in the population size of any species can present significant challenges for their natural recovery, even in instances where degraded habitat is restored. The main barrier to natural recovery in small populations is inbreeding depression: a loss of adaptive potential and overall fitness in populations where interbreeding occurs between closely related individuals (Edmands, 2007). To combat this issue, conservation biologists proposed the idea of genetic rescue through intraspecific hybridization, a process that introduces individuals from outside populations of a species into a threatened local population to encourage an increase in genetic diversity (Zecherle et al., 2021). However, these introductions, either from implementation by conservation managers or the migration of species due to climate change, can dilute genetic adaptations that local populations have evolved to help them survive, a process called outbreeding depression (Edmands, 2007).

Therefore, there is widespread disagreement among biologists and conservation managers about whether inbreeding depression or outbreeding depression poses a bigger challenge to threatened populations (Houde et al., 2011; Todesco et al., 2016). **Modern technologies, especially in genetic and genomic sciences, are a vital tool to answer this question with a diversity of subject taxa and ecosystems. As more data emerges from species that are targeted for genetic rescue or that interbreed with individuals of closely related species from novel range overlapping, it is clear that hybridization is effective in acute population recovery and expands adaptive potential in threatened species.** In an era of climatic uncertainty, allowing for the hybridization of endangered species and managing their recovery as hybrids could prove to be important in maintaining the ecological integrity of the world's most vulnerable ecosystems.

The Case Against Hybridization

Early perspectives rejected both intraspecific and interspecific hybridization as viable conservation strategies because conservation managers expressed caution about the effects of outbreeding depression, historically detrimental to populations of multiple native taxa (Draper et al., 2021). Early conservation initiatives performed intraspecific hybridization by introducing individuals from different geographic locations to supplement a threatened local population. Managers used changes in fitness to monitor the success of local populations after the introduction of outside individuals, which produced negative fitness outcomes in early generations (Barmentlo et al., 2018; Fredrickson et al., 2007; Huff et al., 2011). Three of these reintroduction projects encompassed a variety of taxa (sculpin, primrose, and Mexican wolves) and all showed that breeding pairs consisting of individuals of different subpopulations produced offspring with significantly lower fitness at phenotypic markers compared to breeding pairs composed of individuals of the same subpopulation (Barmentlo et al., 2018; Fredrickson et al., 2007; Huff et al., 2011). For example, Mexican wolf breeding pairs from different subpopulations experienced lower levels of pup survival, a lower number of pups per litter, and a lower number of litters compared to breeding pairs from the same subpopulation (Fredrickson et al., 2007; Figure 1). Also, sculpin offspring produced from parents of different geographic

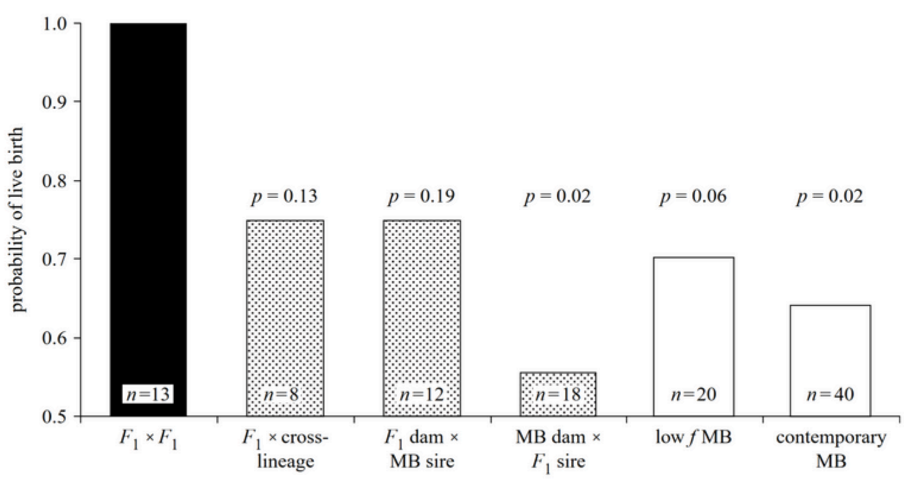


Fig 1. Probability of live birth among Mexican wolf breeding pairs from the same subpopulation (black bar) and breeding pairs from different subpopulations (grey bars) (Fredrickson et al., 2007).

subpopulations were significantly shorter, lighter, and slower growing than those from parents of the same geographic subpopulation (Huff et al., 2011). As shown by these studies, early intraspecific hybridization projects resulted in decreases in fitness across multiple taxa, calling the viability of hybridization in conservation management into question.

While these examples provide evidence supporting early reservations around the mainstream use of hybridization as a conservation strategy, they have temporal limitations that may inflate the effects of outbreeding. When subpopulations of the same species interbreed for the first time, genetic adaptations that each subpopulation has for survival are lost due to outbreeding depression (Houde et al., 2011). However, normal levels of fitness are eventually restored due to the natural selection of adaptively beneficial genes (Houde et al., 2011). This process occurs for multiple generations after the initial introduction, which is longer than the duration of many experiments on the effects of outbreeding in wild populations (Chan et al., 2019). Therefore, early hybridization programs indicate that outbreeding depression is a risk in the translocation of subpopulations into novel ranges, but further research into its long-term effects is needed to characterize the ability of hybridization to rescue species of conservation concern further into the future.

The Viability of Hybridization as a Conservation Strategy

Recent advances in genetic and genomic technologies present a clearer picture of how both intraspecific and interspecific hybridization events have contributed to the evolutionary history of many species and rescued some modern species from rapid declines due to environmental pressures. The first important development arising from the use of modern genetic technologies in hybridization studies is that outbreeding depression can be minimized through the introgression of genetically suitable subpopulations, which can be determined through microsatellite and single nucleotide polymorphism analyses (Weeks et al., 2017). Based on these analyses, subpopulations of mountain pygmy possums across Australia were selected and introduced to a threatened subpopulation, leading to a significant increase in fitness and population size, even in the F1 generation (Weeks et al., 2017). This example highlights the impact of genetic monitoring on the success of controlled hybridization projects for species conservation, thus providing clarity on how these hybridizations may be replicated by managers working with different taxa. When individuals are chosen for hybridization because of their genetic suitability, they have a disproportionately higher impact on the survival and fitness of future generations than do random additions of individuals or the preservation of standing variation for adaptive potential (Hufbauer et al. 2015).

Modern genetic and genomic technologies have also illuminated the evolutionary history of many species, some of which have undergone significant hybridization events to survive changes in environmental conditions. A study of different plant species in New Zealand detailed extensive hybridization among different species in the genus Pachycladon immediately following the end of the Last Glacial Maximum. This hybridization event provided each species with the adaptive potential to improve their defenses against predators and pathogens that were much more prevalent when the climate warmed (Becker et al., 2013). This type of rapid adaptive radiation was also the origin of the vast array of African cichlid species in Lake Victoria, as hybrid offspring interbred with one another to form unique genetic variations in coloration which are vital to their survival in varying states of water quality in the lake basin (Meier et al., 2017). These discoveries point to the long history of adaptations that are introduced between wild populations in times of environmental variability, a process that can be accelerated by the novel introduction of species either through climate change-induced migrations or translocation programs coordinated by conservation managers.

In the current era of climate change and anthropogenic impacts on the environment, both intraspecific and interspecific hybridization events continue to rescue several species from the brink of extinction. In Scandinavia, one immigrant male gray wolf breeding with a female in a local population resulted in temporary increases in population size and offspring fitness compared to contributions from other individuals in the pack which was severely inbred due to anthropogenic barriers and habitat degradation (Å˚ kesson et al., 2016). Similar to the evolutionary history of plants in New Zealand, the climate change-induced spread of diseases like feline immunodeficiency virus (FIV) in degraded environments resulted in a strong degree of introgression between the Scottish wildcat and domestic cats in Scotland. Even though a sharp population decline occurred in Scottish wildcats during this time, due to deaths from FIV and the effects of outbreeding depression with domestic cats, surviving hybrid Scottish wildcats retained the major histocompatibility complex (MHC) of domestic cats that helps their immune system respond effectively to FIV infection (Howard-McCombe et al., 2023). Therefore, since the Scottish wildcat population declined rapidly at the onset of the FIV outbreak, it is unlikely that the population would have been able to acquire immunity to FIV through random mutations of its standing genetic variation, making hybridization a lifeline for species to acquire such adaptations. Hybridization also conferred intermediate levels of immunity to a flatworm infection and a bacterial infection in Atlantic salmon that did not previously show any immunity to these infections (Klemme et al., 2021). Hence, increased disease transmission and habitat degradation can have exceedingly more rapid impacts on wild populations than their current standing genetic variation can account for through beneficial random mutations. This is especially true for threatened and fragmented populations in which standing genetic variation is very low. By facilitating the hybridization of subpopulations and even closely related species, managers can help species adapt to these conditions more efficiently by speeding up the evolutionary process and rescuing declining populations of species that are vital to ecosystem function.

Possible Management Obstacles

Even if hybridization efforts become mainstream in conservation management, legal challenges stand in the way of their implementation, particularly in cases of interspecific hybridization. Both in North America and internationally, many of the major legal protections for threatened and endangered species were created at a time when the prevailing theories viewed hybridization as a threat to the survival of native populations (Draper et al., 2021). As a result, hybridization is either explicitly part of criteria that prohibit conservation programs from obtaining further funding for the conservation of a species or ignored entirely in legislation. For example, the International Union for Conservation of Nature Red List, which determines the demographic status of many species across the world, describes a species as extinct if all individuals of the species are hybrids with other species (Garnett et al., 2011). In addition, important North American conservation policies such as the Endangered Species Act make no mention of hybridized species, as policymakers claim that their conservation would undermine the populations of the two original parent species (Chan et al., 2019).

Current conservation policies displaying these types of biases toward species-centric management may overlook the importance of ecosystem function and resilience to variations in environmental conditions from climate change. If resources are focused on the conservation of individual species that have decreased fitness in this new environmental regime, conservation initiatives will be less effective than if the same number of resources were focused on hybrids that have increased adaptive potential from introgression. By acknowledging adaptively successful hybrids in conservation management initiatives, conservationists can encourage a shift in the legal motivation towards sustaining species populations in a way that best supports the health of their respective ecosystems, responding to the pressures of climate change on ecosystems around the world more accurately.

Conclusions and Future Steps

While outbreeding depression remains a concern for hybridized populations, recent reintroduction projects and genetic studies of evolutionary history suggest that populations can be successfully genetically rescued from extinction after hybridizing with closely related species or individuals from different geographic subpopulations. Hybridization can become the only viable option for populations to adapt quickly enough to changing environmental pressures as shown by the Scottish wildcat and Scandanavian gray wolf examples presented in this paper, signifying its importance as a conservation strategy to increase survival in severely threatened populations (Å˚ kesson et al., 2016; Howard-McCombe et al., 2023). In addition, legal statutes regarding the protection of threatened species should be altered to accommodate for the continued conservation of target species while their populations recover, even if they are hybridized (Chan et al., 2019; Draper et al., 2021).

Future research is needed regarding the level of genetic similarity required for successful hybridization both within and between species of conservation concern, the long-term consequences of outbreeding depression in reintroduction projects, and which species should be prioritized for these projects, as they require a significant number of resources to implement (Edmands, 2007; Zecherle et al., 2021). With targets identified, hybridization can serve as a beacon of hope for threatened species, especially in ecosystems where rapid adaptations to climate change and anthropogenic degradation are required for long-term survival.

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