are bold around humans are also bold around genuine predators and has some empirical support. In addition to the fox squirrel study we reported [3], a more recent experiment on pigeons revealed that those individuals that were bolder and more docile toward humans were also more susceptible to raptor predation [4]. Personality traits are, by definition, repeatable across time and context [5]. Therefore, we expect individuals that have 'positive' early experiences when approaching humans (e.g., obtaining food, passive protection) to develop a boldness syndrome, which may result in bold individuals being more susceptible to predation when exposed to their real predators. Current evidence prevents us from rejecting this plausible outcome. Yet, more research is needed to better understand the conditions under which it is likely.

The positive socioeconomic impacts of nature-based tourism or ecotourism have already been exhaustively discussed in the literature (e.g., [6,7]) and were thus not the focus of our review. We think that it is too simple to say that tourism protects animals from illegal hunting. While providing alternative sources of income for the subsistence of hunters and fishers could permit them to not hunt or fish, we know that highly human-habituated individuals are more vulnerable to human hunters (e.g., [8]). Fitzgerald and Stronza [2] stated that 'Flight initiation distance (FID) is less in areas with tourism because of lack of hunting pressure, not because animals are so habituated they are on their way to domestication'. However, available data do not support this claim. Indeed, many studies have shown reduced FID in areas with more humans than in areas where humans are absent (or less common) even when there is no hunting pressure (reviewed in [9]).

Developing synergies between environmental and socioeconomic objectives depends on many factors, among which is the size of the site. Recent work has shown that bigger attractions (in terms of number of animals) create fewer concerns for both conservation and animal welfare [10]. In addition, wild attractions (e.g., dolphin interactions, gorilla trekking, gibbon watching, polar bear sightseeing) were not only conservation neutral but also significantly decreased animal welfare [10]. Hence, while the socioeconomic benefits for the local human population might be high [11], there is currently no consensus on the environmental impacts of these activities, which might be detrimental [11].

Not all nature-based tourism is ecotourism, but there are three pillars of ecotourism: it should be socially, economically, and environmentally relevant. Our framework focuses exclusively on the environmental relevance. We hope that our study, combined with a recent review [12], will stimulate more research that will permit a better accounting of environmental costs so that the net benefits of eco- and nature-based tourism can be properly identified. In many cases, even with documented environmental costs, we believe that the net benefits will support properly designed tourism. In this sense, there are some likely useful practices to minimize potentially harmful effects of tourism on wildlife[i]. We hope that the framework we developed [1] helps improve nature-based tourism so that the benefits are maximized and the costs to the animals are reduced.

Resource

[i] http://theconversation.com/ecotourism-could-be-making-animals-less-scared-and-easier-to-eat-49196

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Forum

Sex, Mitochondria, and Genetic Rescue

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Genetic rescue is a potentially effective management tool to offset the effects of reduced genetic diversity in imperiled populations. However, implementation requires complex choices. Here we address the consequences of introducing males versus females, highlighting the possibility that introduced females might lead to maladapted mitonuclear genomes and reduced offspring fitness.

Genetic Rescue and Sex Ratio

As we enter the Earth's sixth mass extinction, species are increasingly found in small, fragmented populations, which can suffer from inbreeding depression and a lack of genetic diversity. Infusing genetic variation into such populations via immigrants from another population is termed genetic rescue and has become a widely discussed tool to rescue imperiled populations or species [1,2]. Although genetic rescue is often successful [1,2], there are significant risks, including outbreeding depression. Therefore, genetic rescue remains controversial and its use is rare. For example, Frankham recently highlighted the overall positive effects and low risk of outbreeding depression in previous genetic rescue studies [2]. However, Waller responded that outbreeding depression might have been underestimated due to a lack of data from later generations [3].

Although conceptually simple, genetic rescue is misleadingly complex in practice [4] and many decisions must be made during implementation, including the number and source of introduced individuals. Although guidelines exist for these decisions [5], one important consideration that has received little attention is whether to introduce males, females, or a combination of the two [4]. Sex ratio has important genetic, behavioral, and demographic ramifications, many of which have not been evaluated in the context of genetic rescue [4].

Some genetic effects associated with introducing males versus females are obvious. In species with XY sex determination, only males carry the Y chromosome, which can possess alleles that would benefit the recipient population. Effective population size is also reduced for sex chromosomes, and genes on the non-recombining Y chromosome are especially prone to mutation accumulation, which could affect reproductive success in small populations. The mitochondrial genome is also prone to mutation accumulation because it is typically inherited through the maternal lineage and does not undergo recombination. Therefore, introducing males or females might benefit small populations in which deleterious mutations have accumulated on the Y or mitochondrial chromosomes, respectively [6,7].

Box 1. Propagation of Mitonuclear Incompatibility

When introducing females during genetic rescue, the negative effects predicted to result from mitonuclear incompatibility might not become apparent until later generations. The F_1 generation will have one complete nuclear chromosome from the recipient population paired with one from the introduced population. Therefore, to observe any effect of mitonuclear incompatibility in the F_1 generation, the loci underlying the incompatibility would have to exhibit dominance. In other words, having just one 'mismatched' nuclear allele would have to be sufficient to produce a deleterious effect. However, as these hybrids begin to reproduce, homozygous individuals will segregate out in F_2 and later generations. Eventually, some descendants will have a 'foreign' mitochondrial genome expressed against a largely 'native' nuclear background, resulting in the potential for recessive mitonuclear incompatibilities. The effect is compounded because most hybrid individuals are likely to mate with members of the recipient population (assuming the number of introduced individuals is small relative to the resident population), effectively resulting in paternal backcrosses. This crossing scheme is the same one intentionally used by researchers to generate hybrids showing extreme mitonuclear mismatch during previous experiments [9] and could yield reduced fitness in later generations, which have typically not been monitored in genetic rescue.

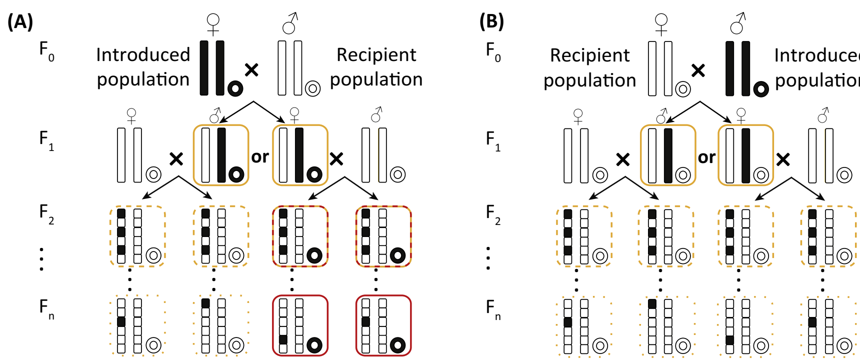

Figure 1. Mitonuclear Incompatibility During Genetic Rescue. (A) When females are introduced during genetic rescue, mitonuclear incompatibilities can be propagated through generations (colored boxes), resulting in reduced fitness, especially in later generations, because females will bring in a novel mitochondrial genome that might be maladapted to the local nuclear genome. (B) Introducing males is less likely to cause mismatch, as their mitochondrial genomes are not transmitted. Each pedigree shows two nuclear chromosomes (linear) and a mitochondrial chromosome (circular). Orange boxes indicate genotypes that are at risk of mitonuclear incompatibilities if a single 'mismatched' nuclear allele is sufficient to have a deleterious effect. Red boxes indicate genotypes that are at risk even if both nuclear alleles must be mismatched with the mitochondrial genome to have a harmful effect. Dashed and dotted lines indicate lower risks associated with a lower overall frequency of mismatched alleles.

Mitonuclear Interactions, Mismatch, and Females

Although others have recognized the potential importance of mitochondrial effects in genetic rescue [6], none have considered the negative effects associated with breaking up coadapted mitonuclear genotypes (Box 1 and Figure 1). There is a growing consensus that within populations mitochondrial and nuclear gene products can be coadapted, largely due to compensatory evolution in the nuclear genome that acts to offset metabolic inefficiency caused by high rates of mitochondrial mutation [8]. Evidence from diverse eukaryotes, including mammals, insects, crustaceans, and yeast, has shown that mitonuclear incompatibilities can cause reduced fecundity, decreased longevity, metabolic deficiencies, lowered stress tolerance, and developmental abnormalities [8,9]. Other studies examining evolutionary rate, introgression, and the protein structure of mitonuclear gene products further support mitonuclear coadaptation and nuclear compensatory evolution, which appear to be ubiquitous across eukaryotes [8,9].

Because the mitochondrial genome is typically inherited maternally and does not recombine, introducing females during genetic rescue could lead to an overlooked form of outbreeding depression via breakdown in the mitonuclear compatibility of offspring. When females are introduced to a recipient population, they contribute a 'foreign' mitochondrial genome that will propagate throughout the population through the maternal lineage, potentially leading to mitonuclear incompatibilities and lowered population fitness, especially in later generations (Figure 1A and Box 1). By contrast, if males are introduced, their foreign mitochondrial genomes are not transmitted. Because the nuclear genome undergoes recombination, incompatibilities resulting from foreign nuclear alleles interacting with native mitochondrial alleles can potentially be eliminated by selection without losing beneficial introduced alleles at other nuclear loci. The net result is a lower expected potential for mitonuclear incompatibility when males are introduced (Figure 1B).

No studies have directly examined the role of mitonuclear interactions in genetic rescue. Interestingly, however, one genetic rescue experiment in guppies documented a more successful outcome when introducing males, but the authors attributed this to behavioral differences between the sexes (see below) rather than mitonuclear interactions [10]. One well-documented case of negative fitness effects resulting from attempted genetic rescue comes from *Tigriopus* copepods, which exhibit severe mitonuclear incompatibilities following hybridization [1,9,11], suggesting that mitochondrial incompatibilities could influence the success of genetic rescue. However, a robust theoretical foundation for genetic rescue that merges relevant demographic and population genetic models remains lacking. Therefore, it is difficult to predict the scenarios under which mitonuclear incompatibility would be most relevant. For example, would introducing a mixed sex ratio alleviate the harmful consequences of introducing females? How severe would mitonuclear incompatibilities need to be to offset the positive effects of genetic rescue? Could genetic rescue fail due to mitonuclear interactions? What is the effect of dominance versus recessiveness for the loci involved in mitonuclear incompatibilities? Does the size of the recipient population and/or relative number of introduced individuals affect the consequences of mitonuclear incompatibilities? Clearly, advancing the theory behind genetic rescue is needed to address these questions.

Behavioral and Demographic Considerations

Although mitonuclear incompatibility could influence the choice of which sex to introduce during genetic rescue, behavioral and demographic differences between sexes can have independent effects, potentially amplifying or counteracting any genetic or mitonuclear concerns. For example, if males are aggressive, territorial, or infanticidal, introducing males could cause more harm, even if mitonuclear incompatibility is severe. Such behavioral considerations led to the exclusive introduction of female Texas cougars during genetic rescue of the Florida panther [12].

Sexual selection could also be important, with mating system and female preference either facilitating or impeding genetic admixture between immigrants and residents. For example, in species in which females prefer novel sexual ornaments and/or males are promiscuous, introducing males could increase the frequency of immigrant–resident mating, which was thought to explain the greater success of introducing males in the aforementioned experimental genetic rescue of guppies [10]. In species with multiple mating by females, immigrant sperm could have an advantage over resident sperm (or vice versa) through sperm competition or sperm selection by females.

From a demographic perspective, introducing females can disproportionately contribute to population survival, as population growth parameters are often more sensitive to the number of females. In addition, using females affords the opportunity to introduce pregnant individuals and thereby magnify the demographic and genetic contributions to the recipient population. Sex-specific dispersion patterns, times to maturity, lifespans, and rates of parasitism/disease could further influence which sex would be the most effective in genetic rescue.

Concluding Remarks

Clearly, deciding which sex to introduce during genetic rescue is complex and requires careful consideration. In light of the possible fitness consequences of mitonuclear incompatibility, we offer the following recommendations. First, empirical studies are needed to determine whether mitonuclear incompatibility plays a role in the risk of failure or the degree of success of genetic rescue efforts and to evaluate its importance relative to behavioral and demographic issues. Second, developing the population genetic theory of genetic rescue and modeling mitonuclear effects in a genetic rescue context would aid in determining which scenarios are most sensitive to these effects. Third, in the absence of more detailed information, one recommendation is to screen donor and recipient populations for similarity at mitochondrial loci and to avoid introducing females with highly divergent mitochondrial haplotypes. Finally, we echo others in calling for continued monitoring of rescued populations throughout later generations [3], when the effects of mitonuclear incompatibility are predicted to be strongest.

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Science & Society

Banning Trophy Hunting Will Exacerbate Biodiversity Loss

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International pressure to ban trophy hunting is increasing. However, we argue that trophy hunting can be an important conservation tool, provided it can be done in a controlled manner to benefit biodiversity conservation and local people. Where political and governance structures are adequate, trophy hunting can help address the ongoing loss of species.

International Outrage over Trophy Hunting in Africa

An American hunter killed a charismatic male lion (*Panthera leo*) called Cecil in Zimbabwe in July 2015. This sparked international outrage, mainly via a storm of social and other media. Several alleged aspects of the hunt itself, such as baiting close to national park boundaries, were done illegally and apparently against the spirit and ethical norms of well-managed trophy hunts. Online outrage had also been sparked earlier in 2015 by the legal hunt of a Critically Endangered male black rhino (*Diceros bicornis*). This hunt was sanctioned by the Namibian Government via an auctioned permit that cost the hunter US$350 000 for the privilege. This outrage arose even though the male was considered 'surplus' to the national black rhino management plan, and the revenue generated from the hunt was to be reinvested into a conservation trust fund to the wider good of conservation in Namibia. These two high-profile hunts and the ensuing public backlash against the ethics and conduct of trophy hunting in general have led to proposals to ban the practice throughout Africa. Furthermore, some commercial passenger and cargo airlines have decided to stop, or may soon stop, the transport of trophies of hunted animals shot legally and sustainably by foreign tourists, irrespective of international conventions, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and national laws that allow trophy hunting.

Hunting Industry in Sub-Saharan Africa

Trophy hunting strongly contributes to the conservation enterprise in sub-Saharan Africa, where large areas support important terrestrial biodiversity that is currently allocated to trophy hunting use (Table 1). While most of the hunted individuals (e.g., 96% in South Africa in 2012) [1] are often from more common and less valuable species (Table 1), most of the trophy hunting revenue is generated from a few species carrying valuable trophies, particularly the charismatic 'Big Five' (lion leopard *Panthera pardus*; elephant *Loxodonta africana*; buffalo *Syncerus caffer*; and black or white rhinoceros *Ceratotherium simum*) [2]. Out of the US$68 million of gross revenue generated from trophy hunting in South Africa in 2012, over US$28 million (at least 41%) was generated from the Big Five alone (i.e., $5 635 625 from 635 buffaloes; $1 194 600 from 33 elephants; $647 500 from 37 leopards; $15 270 750 from 617 lions, $300 000 from one black rhinoceros; and $5 355 000 from 63 white rhinoceroses) [1]. Southern African countries and Tanzania exported most of the Big Five trophies between 2009 and 2013 (Figure 1). At the same time, two countries that do not typically attract many tourists (the Central African Republic, currently undergoing a conflict, and Cameroon, where poaching pressure is high) allowed trophy hunting of big cats and elephants, respectively, over the same period (Figure 1).

Concerns about Trophy Hunting

Overall, land allocated to trophy hunting has the potential to assist countries to achieve biodiversity conservation goals [3]. However, the contribution of hunting to conservation is often contentious for various reasons. There can be uncertainty over the sustainability of offtake rates and their potential impact on wildlife populations [4]. This concern arises because quotas and offtakes are not often based on scientific assessments. Furthermore, restrictions on the age of hunted