Contributed Paper

Long-term demographic and genetic effects of releasing captive-born individuals into the wild

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Abstract: Because of continued habitat destruction and species extirpations, the need to use captive breeding for conservation purposes has been increasing steadily. However, the long-term demographic and genetic effects associated with releasing captive-born individuals with varied life histories into the wild remain largely unknown. To address this question, we developed forward-time, agent-based models for 4 species with long-running captive-breeding and release programs: coho salmon (Oncorhynchus kisutch), golden lion tamarin (Leontopithecus rosalia), western toad (Anaxyrus boreas), and Whooping Crane (Grus americana). We measured the effects of supplementation by comparing population size and neutral genetic diversity in supplemented populations to the same characteristics in unaltered populations 100 years after supplementation ended. Releasing even slightly less fit captive-born individuals to supplement wild populations typically resulted in reductions in population size and genetic diversity over the long term when the fitness reductions were heritable (i.e., due to genetic adaptation to captivity) and populations continued to be regulated by density-dependent mechanisms over time. Negative effects for species with longer life spans and lower rates of population replacement were smaller than for species with shorter life spans and higher rates of population replacement. Programs that released captive-born individuals over fewer years or that avoided breeding individuals with captive ancestry had smaller reductions in population size and genetic diversity over the long term. Relying on selection in the wild to remove individuals with reduced fitness mitigated some negative demographic effects, but at a substantial cost to neutral genetic diversity. Our results suggest that conservation-focused captive-breeding programs should take measures to prevent even small amounts of genetic adaptation to captivity, quantitatively determine the minimum number of captive-born individuals to release each year, and fully account for the interactions among genetic adaptation to captivity, population regulation, and life-history variation.

Keywords: artificial selection, captivity, domestication, genetic adaptation, supplementation

Efectos Genéticos y Demográficos a Largo Plazo de la Liberación de Individuos Nacidos en Cautiverio

Resumen: Debido a la continua destrucción de hábitats y a la extracción de especies, la necesidad de utilizar la reproducción en cautiverio con motivos de conservación ha aumentado constantemente. Sin embargo, los efectos genéticos y demográficos a largo plazo asociados con la liberación de individuos nacidos en cautiverio con historias de vida variadas permanecen en gran parte desconocidos. Para responder a la pregunta anterior desarrollamos modelos de tiempo futuro basados en agentes para cuatro especies con programas de reproducción en cautiverio y liberación con una larga duración: el salmón plateado (Oncorhynchus kisutch), la marmoseta dorada (Leontopithecus rosalia), el sajó occidental (Anaxyrus boreas), y la grulla trompetera (Grus americana). Medimos los efectos de la suplementación al comparar el tamaño poblacional y la diversidad genética neutra en las poblaciones suplementadas con las mismas características en poblaciones sin alteraciones 100 años después de la suplementación. La liberación de individuos criados en cautiverio con una mínima aptitud física como suplemento para las poblaciones silvestres resultó típicamente en la reducción del tamaño poblacional y de la diversidad genética a largo plazo cuando la reducción en la aptitud fue heredable (es decir, debido a la adaptación genética al cautiverio) y las poblaciones siguieron

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Article impact statement: Small amounts of genetic adaptation to captivity may negatively impact long-term wild population size and genetic diversity.

Paper submitted April 4, 2018; revised manuscript accepted August 28, 2018.
reguladas a lo largo del tiempo por los mecanismos dependientes de la densidad. Los efectos negativos para las especies con ciclos de vida mayores y tasas más bajas de reemplazo poblacional fueron menores que para aquellas especies con ciclos de vida más cortos y tasas más altas de reemplazo poblacional. Los programas que liberaron individuos criados en cautiverio durante menos años o que evitaron reproducir individuos con descendencia en cautiverio tuvieron reducciones menores en el tamaño poblacional y en la diversidad genética a largo plazo. La dependencia de la selección silvestre para extirpar a los individuos con aptitud física reducida mitigó algunos efectos demográficos negativos, pero a un precio sustancial para la diversidad genética neutra. Nuestros resultados sugieren que los programas de reproducción en cautiverio enfocados en la conservación deberían tomar medidas para prevenir las más mínimas cantidades de adaptación genética al cautiverio, determinar cuantitativamente el número mínimo de individuos nacidos en cautiverio para liberar cada año, y compensar totalmente las interacciones entre la adaptación genética al cautiverio, la regulación poblacional, y la variación en historias de vida.

Palabras Clave: adaptación genética, cautiverio, domesticación, selección artificial, suplemento

Introduction

The total number of species bred in captivity has increased considerably over the past 50 years, and recent predictions suggest that several thousand additional species may soon require captive breeding in order to prevent extinction (Seddon et al. 2005; Mendelson et al. 2006; Attard et al. 2016). Because the primary goal of many conservation-focused captive breeding programs is to rehabilitate declining or extinct populations, a greater reliance on captive breeding will ultimately increase the total number of captive-born individuals released back into the wild (Toone & Wallace 1994; Russell et al. 1994i). However, the long-term effectiveness of releasing captive-born individuals into wild environments remains largely unknown because many captive-breeding programs have been initiated relatively recently and thus long-term data are often not available. It is challenging to obtain reliable multigeneration estimates of lifetime reproductive success necessary for evaluating wild populations before, during, and after the release of captive-born individuals, and even if estimates of fitness could be obtained, it may be difficult to disentangle confounding factors, such as changes in habitat quality through time and uncertain genetic ancestry (Fraser 2008; Muhfeld et al. 2009; Willoughby & Christie 2017).

Despite the challenges associated with evaluating the long-term effectiveness of captive-breeding programs, numerous studies have documented short-term reductions in fitness for captive-bred individuals after release into the wild (Araki et al. 2008; Christie et al. 2014; reviewed in Williams & Hoffman 2009). Recent empirical work has further revealed that these reductions in fitness can occur after a very brief period of captive breeding (Schroder et al. 2008), sometimes after only 1 generation in captivity (Araki et al. 2007; Christie et al. 2012a). Because reductions in fitness associated with captive breeding often have a heritable component there may be substantial long-term demographic and genetic consequences for wild populations (Lynch & O’Hely 2001; Ford 2002; Baskett et al. 2013). Although empirical findings illustrate that captive-born individuals can have reduced fitness in the wild, the interactions among genetic adaptation to captivity, population regulation, and subsequent fitness upon reintroduction into the wild remain unknown for populations or species with varied life histories.

Genetic adaptation to captivity is the response to selection that increases the fitness of individuals in a novel captive environment (Frankham 2008). Although genetic adaptation to captivity increases the fitness of individuals in the captive environment, those same individuals often have decreased fitness in the wild environment.
(Christie et al. 2012a). It may be possible to minimize the amount of genetic adaptation to captivity by limiting the number of generations individuals are held in captivity (Frankham 2008), equalizing family sizes (Allendorf 1993), lowering rearing densities (Frankham & Loebel 1992), and minimizing differences between captive and wild environments (Shuster et al. 2005). However, each of these efforts require considerable resources, and it is critical to know how much effort should be devoted to minimizing genetic adaptation to captivity versus addressing other challenges faced by captive-breeding programs (e.g., inbreeding; Witzenberger & Hochkirch 2011). Furthermore, different species may adapt to captivity at different rates, and even similar rates of genetic adaptation may translate into large differences in long-term effects of captive breeding due to differences in life-history traits. For example, differences in fecundity and generation time between species may not only affect the rate of genetic adaptation to captivity (Williams & Hoffman 2009) but may also affect the long-term population trajectories on release back into the wild.

Captive breeding for conservation is typically used to supplement declining populations or to reintroduce individuals in order to reestablish a previously extirpated population. We broadly define population supplementation (or “supportive breeding” [Ryman & Laikre 1991]) as releasing captive-born offspring into a declining population to provide that population with a temporary demographic boost until the causes of the population decline can be remedied (Allendorf et al. 2013). Within this broad definition, we did not directly consider programs that release individuals accidentally or for purposes of subsequent harvest (Baskett et al. 2013). In practice, there are often competing goals within a single captive-breeding program (Naish et al. 2007; Christie et al. 2012b), but many goals focus on the successful introduction of captive-born individuals into the wild with the expectation that captive-released individuals will survive and pass on their genes to subsequent generations. For declining populations that are no longer maintained by density dependent processes (Hixon & Johnson 2009), the release of captive-born individuals is often seen as a last-ditch effort to keep the populations persisting until carrying capacities can be increased and population regulation restored (Snyder et al. 1996). In those cases, the short-term consequence of not acting (e.g., extinction) outweigh any long-term considerations. However, some populations have experienced a reduction in carrying capacity (e.g., habitat destruction) but continue to be regulated by density dependent processes (Lorenzen & Enberg 2002; Cubaynes et al. 2014). We focused on these populations because the long-term effects of supplementation may outweigh the short-term benefits.

Because of the challenges associated with empirically measuring the long-term effects of captive breeding, including identifying appropriate control populations, we developed forward-time agent-based models to characterize captive-breeding programs and the release of captive-born individuals into wild populations. Specifically, we measured changes in the population sizes and neutral genetic diversity of wild populations managed with captive-breeding based conservation programs. Within our models, we systematically varied the extent of genetic adaptation to captivity to address 3 questions. How much genetic adaptation to captivity can occur before there are long-term effects on population size and neutral genetic diversity? What are the differences in long-term population sizes for species with different life-history characteristics? What are the long-term effects of different captive breeding and release strategies? We compared all results with identical control populations that had no captive-breeding programs and considered the effects of changes in the number of captive-born individuals released into the wild, the extent of captive ancestry in individuals selected for captive breeding, and the immigration of individuals from surrounding populations.

**Methods**

To identify the long-term impacts of releasing captive-born individuals into the wild, we developed a forward-time agent-based model that is both age and stage-structured, fully accounts for overlapping generations, and tracks individuals and their multi-locus genotypes over the course of 250 years (Fig. 1). We considered 4 species, all of which have been subject to extensive captive breeding and release efforts: coho salmon (*Oncorhynchus kisutch*), western toad (*Anaxyrus boreas*), Whooping Crane (*Grus americana*), and golden lion tamarin (*Leontopithecus rosalia*). These species were chosen because they possess life-history characteristics that allowed us to systematically examine the long-term effects of differences in generation time (i.e., life span and maturation rate) and fecundity (Table 1). To systematically evaluate parameters, we utilized a default set of parameter values and varied parameters of interest independently. We modeled supplementation by allowing captive-born individuals to be released into the source population from which their parents were collected. The basic model is described here in the text and details are in Supporting Information.

Simulations began without captive breeding and the population at carrying capacity where all individuals (total population size = 500, Supporting Information) were characterized by 50 polymorphic microsatellite loci. These loci were used to characterize changes in neutral genetic diversity associated with supplementation. The model began with reproduction in the wild (Fig. 1), where reproduction occurred between randomly selected pairs of adults. All offspring were assigned genotypes in accordance with Mendelian inheritance, where
Figure 1. Schematic representation of the age- and stage-structured population supplementation models: (a) steps in wild-population model (reproduction, density-dependent mortality, density-independent mortality, growth of all individuals regardless of ancestry, and additional chance of mortality for individuals that had reduced fitness in the wild due to captive ancestry) (every generation, 1 effective migrant from a large, neighboring population was introduced); (b) steps in captive-breeding model (all captive parents were wild-born individuals collected as adults, were only used in a single pair, and were never used for more than 1 year), and (c) effects of supplementation scenarios in which individuals born in captivity were added to the wild population to bolster population size. All scenarios were compared with control runs in which the model progressed as in (a), except that a captive-breeding program was never initiated.

Table 1. Life-history characteristics of modeled species subjected to extensive captive-breeding and release programs focused on conservation.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Class</th>
<th>Maximum offspring</th>
<th>Maximum life span (years)</th>
<th>Age at maturity (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coho salmon</td>
<td>Oncorhynchus kisutch</td>
<td>Actinopterygii</td>
<td>100</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Western toad</td>
<td>Anaxyrus boreus</td>
<td>Amphibia</td>
<td>30</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Whooping Crane</td>
<td>Grus americana</td>
<td>Aves</td>
<td>1</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>Golden lion tamarin</td>
<td>Leontopithecus rosalia</td>
<td>Mammalia</td>
<td>2</td>
<td>8</td>
<td>2</td>
</tr>
</tbody>
</table>

*Maximum number of offspring produced in a single year that can survive to adulthood.
1 allele at each locus was randomly selected from each parent. We assigned the number of offspring produced per pair using a random deviate from a gamma distribution (Supporting Information). To determine the total number of offspring to create in the wild, we estimated population size in the following year using the logistic growth equation and further modified this value using an estimate of density independent effects (e.g., environmental variation) (Supporting Information). We also included a single effective migrant per generation (subsequently varied from 1–10 migrants that were included every 1–10 years, Supporting Information) randomly pulled from a separate pool of 10,000 individuals created at the beginning of each simulation to approximate drift-migration equilibrium in the supplemented population. We assumed an individual’s cumulative probability of mortality, in any given year, was equal to the quotient of an individual’s age and the maximum life span of the species. Individuals selected for mortality were removed from the model and we incremented all surviving individuals’ ages by 1.

After allowing the wild population to persist uninterrupted for 75 years to permit stabilization of age structure and genetic diversity in all species, we next created and managed a captive population alongside the wild population that consisted of wild-born adults and their captive-born offspring (Fig. 1b). Prior to reproduction in the wild, 15% of the reproductively mature adults were randomly selected for use in the captive population (proportion of captive breeders; Supporting Information). To determine if any long-term effects were simply due to the removal of adults from the population, we also examined the effects of removing adults without the subsequent release of captive-born offspring. Each year, we required an entirely new set of captive breeders to be collected from the wild. Only wild-born individuals were used as captive parents to minimize the effects of inbreeding and genetic drift on neutral genetic diversity (genetic adaptation to captivity) (Supporting Information). We assumed that fitness is determined by a heritable trait (e.g., growth rate), but we do not model those traits directly because those traits would vary across species and captive-breeding programs, selection can act on multiple and varied traits through time, and we were most interested in the relative effects across species while controlling for the amount of genetic adaptation to captivity. We used the fitness parameter to influence pre-reproduction mortality within the population by removing individuals at a probability equal to their fitness estimate. The fitness parameter of captive-born offspring was modified by reducing the assigned fitness (fitness reduction range = 0–0.3 [Supporting Information]). When not being systematically varied we adopted fitness reduction of 0.1 as a default value, which is on the low end of fitness reductions associated with supplementation (Araki et al. 2007; reviewed in Christie et al. 2014). As years progressed, if an individual selected for captive breeding had previous captive ancestry, resulting offspring would still receive the same incremental fitness reduction applied by the model. For example, if an individual with captive ancestry had a fitness reduction of 0.1 and was mated in captivity to an individual with no captive ancestry then their offspring would have a mean fitness reduction of 0.15 (i.e., $\frac{0.1+0.1}{2} + 0.1$). We later limited the extent to which captive ancestry can accumulate over generations by setting a maximum fitness reduction associated with genetic adaptation to captivity.

To investigate whether selection in the wild can mitigate the heritable fitness reductions associated with captive breeding we modified the effects of selection in the wild. First, we varied heritability by modifying the standard deviation of the normal distribution used to...
assign fitness (individual fitness was generated from the mean parental fitness [Supporting Information]). We used a small standard deviation to model high heritability and increased the standard deviation to model lower heritability. Finally, we increased directional selection by only allowing individuals that exceeded a minimum fitness threshold to reproduce in the wild each year (i.e., we set minimum fitness requirements [Supporting Information]). Our minimum fitness thresholds were relative to the yearly mean population fitness and were varied from 0.001% to 1.000%.

We compared the impacts of all tested parameters on population size and genetic diversity by comparing the output of the simulated populations to control simulations. We generated independent controls using the same parameter sets from each experimental simulation except for eliminating captive breeding from the control simulations. As a basis for comparison, we also measured the effects of removing individuals for captive breeding, but not releasing their offspring back into the wild, in all 4 species. For each unique parameter set, we determined the population size and the average number of alleles, 100 years after captive breeding ended (year 225). Finally, we estimated the mean and 95% confidence interval (CI) around the mean of the difference in population size and average number of alleles per locus between the control and the supplemented populations across the range of parameter values tested. We ran 100 replicates for each unique combination of parameters where simulations were run in R version 3.2 (R Development Core Team 2014) on a high-performance computing cluster.

Results

For control simulations where we removed individuals for captive breeding but did not release any offspring back into the wild, there was no reduction in long-term mean population fitness; population sizes decreased while individuals were collected for use in captive breeding but immediately rebounded; and genetic diversity initially declined, but then rebounded over time (Fig. 2). We observed different population effects when captive-born individuals were released into wild populations. Supplementation of the wild population using captive-born individuals resulted in a rapid, population-wide decrease in mean fitness. For example, when captive-born individual fitness was reduced by an average of 10%, the mean population fitness always dropped below 0.8 prior to the end of supplementation (Fig. 3). The final mean population fitness was lower than the mean population fitness after supplementation (Fig. 3). The observed reduction in genetic diversity was related to the size of the demographic decrease that occurred for each species; a large population size decrease after supplementation was followed by a large decrease in genetic diversity (cf. salmon to Whooping Cranes) (Fig. 3). The loss of genetic diversity was not mitigated by increasing the number of effective migrants from large, adjacent populations, as even 10 effective migrants each year could not restore genetic diversity (Supporting Information).

Neutral genetic diversity was also consistently reduced long after the release of captive-born individuals had been stopped (Fig. 3). The observed reduction in genetic diversity was related to the size of the demographic decrease that occurred for each species; a large population size decrease after supplementation was followed by a large decrease in genetic diversity (cf. salmon to Whooping Cranes) (Fig. 3). The loss of genetic diversity was not mitigated by increasing the number of effective migrants from large, adjacent populations, as even 10 effective migrants each year could not restore genetic diversity (Supporting Information).

Across all simulated fitness reductions (i.e., 0–0.3), all 4 species had a population size reduction that was proportionately larger than the decrease in fitness due to captive breeding (Fig. 4a). As little as a 2.5% yearly reduction in fitness due to genetic adaptation to captivity lead to a long-term population size reduction of up to 20%. Species-specific patterns were related to maximum life span, as species with the shortest life spans (golden lion tamarin and coho salmon, 8 and 7 years, respectively), had larger population size reductions relative to the longer-lived species. We found a similar relationship for genetic diversity (Fig. 4b). Reductions in genetic diversity were less extreme at all reduced fitness values, relative to the population size reductions observed. Although Whooping Cranes were below the 1:1 line, all other species suffered disproportionately large reductions in genetic diversity (Fig. 4b). When genetic adaptation to captivity was low (i.e., fitness reductions were small), supplementation could occasionally increase neutral genetic diversity in populations (for an empirical example see Willoughby et al. 2018).

Population size and genetic reductions associated with adaptation to captivity were minimized when captive programs limited the accumulating effects of genetic adaptation to captivity or when the duration and frequency of supplementation were reduced (Fig. 5 & Supporting Information). The continual decreases in
Figure 2. Long-term trajectories for relative fitness, population size, and neutral genetic diversity in wild populations of (a, b, c) Whooping Crane, (d, e, f) golden lion tamarin, (g, h, i) western toad, and (j, k, l) coho salmon before (years 50–75), during (years 75–125), and after (years 125–250) the removal of wild-born adults for use in captive breeding each year when there was no release of captive-born offspring into the wild. Control populations (populations with no adults removed) are shown behind the adult-removed population lines. Simulations were run with the default parameters (see Supporting Information). Shading in years 75–125 indicates the years during which adult removal occurred. Genetic diversity is illustrated as the relative number of alleles per locus calculated relative to the mean number of alleles present each year in the simulations lacking captive breeding.
Figure 3. Long-term trajectories for relative fitness, population size, and neutral genetic diversity in wild populations of (a, b, c) Whooping Crane, (d, e, f) golden lion tamarin, (g, h, i) western toad, and (j, k, l) coho salmon before (years 50–75), during (years 75–125), and after (years 125–250) the introduction of captive-born individuals. Control populations (populations with no adults removed) are shown behind the supplementation lines. Simulations were run with the default parameters (see Supporting Information). Shading in years 75–125 indicates the years during which supplementation occurred. Genetic diversity is illustrated as the relative number of alleles per locus calculated relative to the mean number of alleles present each year in the simulations lacking captive breeding. We assumed genetic adaptation to captivity resulted in a 10% yearly reduction in fitness to highlight key differences among species. Smaller reductions in fitness, which may be more realistic for some programs, are illustrated in Figs. 4 and 5.
population fitness during supplementation did not occur when the amount of captive ancestry was limited in the captive breeders, resulting in a population size that was minimally reduced (Fig. 5a & Supporting Information). We also evaluated the effects of reducing the duration of supplementation and of altering the frequency of supplementation over 50 years (Fig. 5b & Supporting Information). Both population size and genetic reductions measured 100 years after supplementation were smaller with fewer years of supplementation or when fewer captive-release events occurred (Fig. 5b). Across a wider range of supplementation periods (1–50 years), reductions in population sizes scaled linearly to the number of years of supplementation for all species (Fig. 5c). Less genetic diversity was lost when supplementation occurred over a relatively short period (Supporting Information).

Across all species, no level of selection was sufficient to result in a change in population size or genetic diversity when heritability in the wild was low (Supporting Information). Increasing the strength of selection when heritability was high resulted in a decrease in the long-term population size reductions associated with releasing captive-born individuals (Supporting Information). However, increasing the intensity of selection increased the loss of neutral genetic diversity (Supporting Information), illustrating a trade-off between long-term population sizes, neutral genetic diversity, and selection.

Discussion

Although supplementation programs are a common and sometimes necessary solution for threatened and endangered species recovery (Seddon et al. 2005), we found that releasing captive-born individuals into the wild can have long-lasting and negative demographic and genetic effects when genetic adaptation to captivity has a heritable basis and when declining populations continue to be regulated by density-dependent mechanisms. Under these conditions, most populations did not return to their prior level of abundance when captive-born individuals had reduced fitness in the wild. Of particular concern is the observation that even small yearly reductions in fitness associated with captive breeding (e.g., 2.5%) led to substantial long-term declines in population sizes. Because the statistical power to detect small changes in fitness (i.e., <10%) due to captive breeding can be low (Christie et al. 2014), there may be undetected fitness consequences of present-day captive-breeding programs that will influence the future demographic and genetic trajectories of supplemented populations. Reviews of supplementation programs in salmon suggest that early-generation captive-born individuals can have up to 50% reductions in reproductive success compared with their wild-born counterparts (Araki et al. 2008; Christie et al. 2014). If even a small portion of that reduction in fitness is due to genetic adaptation to captivity, then there may be substantial long-term demographic and genetic effects for the targeted populations.

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For all 4 species, increasing the amount of genetic adaptation to captivity resulted in greater decreases in long-term population sizes and genetic diversity in both supplemented and reintroduced populations. The relationship between genetic adaptation to captivity and long-term population size was not strictly linear in supplemented populations and the associated population size reduction was greater than a 1:1 relationship (Fig. 4a), illustrating that reduced fitness associated with genetic adaptation to captivity can cause disproportionately large reductions in population sizes. Additionally, there was less of a proportional reduction in genetic diversity than population sizes (Fig. 4b). However, we replaced captive breeders each year. If we had used isolated, captive populations for multiple generations, as is often done in practice, the increased mating between relatives and increased genetic drift would exacerbate the observed reduction in neutral genetic diversity (Haig et al. 1990; Lacy 2009; Willoughby et al. 2017).

We also identified differences in response to supplementation that was related to species life-history differences. Life-history characteristics that resulted in the
largest long-term decreases in population sizes and genetic diversity were also related to increased rates of genetic adaptation to captivity (Fraser 2008). This means that species with short generation times and high rates of population replacement will be more likely to genetically adapt to captivity and, upon release into the wild, more likely to have long-term reductions in population sizes and genetic diversity compared with longer-lived species. As such, many species of invertebrates, fishes, amphibians, and small birds and mammals, are at high risk for long-term reductions in population size and genetic diversity associated with genetic adaptation to captivity.

Limiting the extent to which negative, heritable fitness effects accrue over several generations of captive breeding can be effective at reducing the long-term reductions in population sizes and genetic diversity (Fig. 5). There are at least 3 related ways that this mechanism could be implemented in practice, each of which has its own set of challenges. The first approach is to simply breed individuals with no captive ancestry (Lynch & O’Hely 2001; Ford 2002). This approach is challenging because it can be difficult to identify individuals with no captive ancestry and it does not take a long period of time for all individuals in a population to have at least some amount of captive ancestry (Baskett et al. 2013). Second, management decisions could be implemented that extend the length of time that individuals with no captive ancestry remain in the wild population. For example, supplementation programs could reduce gene flow into the wild population by releasing fewer offspring or releasing offspring at a reduced frequency (Supporting Information).

Although effective in the long term, limiting the number of captive-offspring released may reduce the short-term, demographic benefits of supplementation. Third, captive-breeding programs could adopt cryopreservation strategies, such that individuals with no captive ancestry could be used at a later point in time (Johnston & Lacy 1995). However, there may be considerable economic costs associated with this strategy and there may be other unknown deleterious effects (Swanson 2006; Andrabi & Maxwell 2007). Thus, while limiting the amount of captive ancestry in the captive population can be a very effective strategy, there are many challenges for successfully implementing this practice.

In addition to modeling differences in life-history variation, we assumed that the reduction in fitness had a heritable, genetic basis, which we think is a safe assumption even if it does not explain all of the reductions in fitness observed empirically (Araki et al. 2007; Frankham 2008; Christie et al. 2012a, 2014, 2016). We also assumed that the populations continued to be regulated by density-dependent processes and the validity and implications of this assumption deserve further attention. If, on the one hand, populations can no longer be self-regulating, then supplementation efforts are warranted as they may prevent extinction over the short term. Of course, if the factors that have resulted in the loss of population regulation are not eventually reversed, the population will never become self-sustaining. On the other hand, many populations may incur substantial reductions in carrying capacity, prompting immediate conservation action, but could still be regulated by density dependent processes.
In these cases, if the conservation action ends up resulting in supplementation with captive-born individuals, the long-term effects of may be worse than if no action was taken. Thus, further priority should be given to determining the carrying capacity and the respective strengths of density dependent and density independent processes before releasing captive-born individuals back into the wild.

Our results illustrate that even small amounts of genetic adaptation to the captive environment can result in substantial, long-term reductions in population sizes and neutral genetic diversity. However, this concerning result does not necessarily mean that all conservation-focused captive-breeding programs should be eliminated or that captive breeding per se cannot be a useful tool. In fact, there are several cases where releasing captive-born individuals has been beneficial to wild populations (e.g., black-footed ferrets, Mustela nigripes [Russell et al. 1994], sockeye salmon, Oncorhynchus nerka [Kline & Flagg 2014]). In light of our results, however, we believe that the current status quo for captive-breeding programs should be amended. First, we recommend that new techniques for preventing genetic adaptation to captivity should be further developed and refined (e.g., Berejikian & Van Doornik 2018). Second, we recommend that all supplementation programs estimate carrying capacities and the strength of population regulation. If supplementation is deemed necessary, we further recommend a priori calculations for the minimum number of captive-born individuals that need to be released to meet conservation goals. Releasing more captive-born individuals than needed is likely to exacerbate negative demographic and genetic effects (Supporting Information). We also agree with prior assessments that rigorous and, where possible, quantitative cost-benefit analyses be performed before releasing captive-born individuals (Lindburg 1992; Waples & Do 1994), allowing for the possibility that the best course of action may be to not use supplementation. Finally, we urge captive-breeding programs to adopt a long-term perspective. When faced with rapidly declining populations or potential species extinctions, it is challenging to take a long-term view but doing so may help turn short-term gains into long-lasting conservation success.

Acknowledgements

We thank M. Blouin, M. Ford, A. Harder, A. Martinez, L. LaRue, and M. Sundaram for helpful conversations and advice regarding the development of these research ideas. This research was made possible, in part, through computational resources provided by the Purdue University Rosen Center for Advanced Computing and by the Departments of Biological Sciences and Forestry and Natural Resources.

Supporting Information

Details of simulation methods including allele frequency specifications, identification of reproductive pairs, determination of reproductive success, and results specific to the effects of life span and time to maturity in Whooping Cranes (Appendix S1) and parameter values used in simulations and the effects of varying the ratio of captive offspring released to wild offspring born, altering number and frequency of migrants, limiting the accumulation of genetic adaptation to captivity, reducing the supplementation period, combining the effects of limiting genetic adaptation to captivity and reducing supplementation period, varying the supplementation interval, reducing heritability of fitness, and increasing the intensity of selection in the wild are available online (Appendix S2). The authors are solely responsible for the content and functionality of these materials. All simulation and plotting code is available via GitHub (https://github.com/purdue.edu/MarkRChristieGroup/captivebreeding-IBM). Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Berejikian BA, Van Doornik DM. 2018. Increased natural reproduction and genetic diversity one generation after cessation of a steelhead trout (Oncorhynchus mykiss) conservation hatchery program. PLOS ONE 13 (e0190799) https://doi.org/10.1371/journal.pone.0190799.
Captive Breeding

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