Brief Communication

Captive Ancestry Upwardly Biases Estimates of Relative Reproductive Success

Janna R. Willoughby and Mark R. Christie

From the Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, IN 47907-2054 (Willoughby and Christie); and Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN (Christie).

Address correspondence to J. R. Willoughby at the address above, or e-mail: willoughby@purdue.edu.

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Abstract

Supplementation programs, which release captive-born individuals into the wild, are commonly used to demographically bolster declining populations. In order to evaluate the effectiveness of these programs, the reproductive success of captive-born individuals released into the wild is often compared to the reproductive success of wild-born individuals in the recipient population (relative reproductive success, RRS). However, if there are heritable reductions in fitness associated with captive breeding, gene flow from captive-born individuals into the wild population can reduce the fitness of the wild population. Here, we show that when captive ancestry in the wild population reduces mean population fitness, estimates of RRS are upwardly biased, meaning that the relative fitness of captive-born individuals is over-estimated. Furthermore, the magnitude of this bias increases with the length of time that a supplementation program has been releasing captive-born individuals. This phenomenon has long-term conservation impacts since management decisions regarding the design of a supplementation program and the number of individuals to release can be based, at least in part, on RRS estimates. Therefore, we urge caution in the interpretation of relative fitness measures when the captive ancestry of the wild population cannot be precisely measured.

Subject area: Conservation genetics and biodiversity

Keywords: captive breeding, domestication, genetic adaptation, hatchery, selection, supplementation

A growing number of species face significant threats to their continued survival: 26% of animals, and 58% of plants evaluated by the International Union for the Conservation of Nature are considered threatened or are extinct in the wild (IUCN 2016). Although species can be vulnerable to extinction for a variety of reasons (e.g., small number of adults, small geographic ranges; Willoughby et al. 2015), contemporary declines in population size often prompt immediate conservation actions, such as population supplementation (also known as supportive breeding; Ford 2008). Population supplementation is the release of captive-born offspring into the wild in order to provide a temporary demographic increase to the wild population (Reisenbichler and Rubin 1999; Allendorf and Luikart 2007).

Although there can be other goals identified within a single captive breeding program (Waples and Drake 2004; Naish et al. 2007; Christie et al. 2014a), supplementation programs typically focus on the successful survival and reproduction of captive-born individuals released into the wild (Russell et al. 1994; Toone and Wallace 1994; van Dierendonck et al. 1996).

Tracking captive-born individuals that are released into wild populations over time is critical for ensuring that conservation efforts are effective (Lowe et al. 2015). Although counting the number of released individuals that survive until maturity is a useful approach for quantifying supplementation success, reliance on these methods alone can result in an incomplete picture when captive-born...
individuals have reduced reproductive success in the wild. Therefore, an additional approach for quantifying the success of supplementation is to measure the reproductive success of individuals in the recipient, wild population (Kalnowski and Taper 2005). Relative reproductive success (RRS) compares the fitness of captive-born and wild-born individuals when both groups reproduce in the same wild population (Cuenco 1994). To maximize the demographic gains associated with supplementation, individuals released from captive populations would ideally have the same fitness as their wild-born counterparts, resulting in an RRS equal to one. However, empirical estimates show that fitness is often lower for captive-born individuals compared to wild-born individuals, resulting in an RRS that is less than one (Araki et al. 2008; Christie et al. 2014b).

Despite the quantifiable reduction in RRS documented in supplemented populations, RRS may be upwardly biased in some situations. When captive-born individuals reproduce with wild-born individuals, as is intended in many supplementation programs, captive ancestry increases in the wild population (i.e., there is gene flow from the captive population to the wild population). If captive-born individuals have heritable reductions in fitness, for which there is mounting empirical evidence (Araki et al. 2009; Christie et al. 2012a; Ford et al. 2016), reproduction between captive-born individuals (or their descendants) and wild individuals will reduce the mean fitness of the wild population (Reisenbichler and Rubin 1999; Lynch and O’Healy 2001). This reduction in the fitness of the wild population means that the true fitness of wild-born individuals will be consistently underestimated due to the increased captive ancestry present in wild-born individuals (relative to the fitness of individuals if a supplementation program had never been initiated). Fitness reductions in the wild population can occur during a single supplementation period that occurs over a number of years, where captive ancestry can gradually increase in the wild population. Additionally, if the wild population already contains some captive ancestry from prior supplementation programs, wild population fitness may already be reduced, potentially leading to a bias in RRS estimates.

Here, we systematically examine how much captive ancestry biases estimates of RRS. Specifically we ask, what is the difference between RRS when the wild population has captive ancestry compared to when the wild population contains only individuals with no captive ancestry? To address this question, we used an individual-based model to simulate the supplementation of wild populations using a captive breeding program. We found that, as captive ancestry increased in the wild population, wild population fitness decreased proportionate to the amount of genetic adaptation to captivity, and this change in wild population fitness led to an upwardly biased estimate of supplementation effectiveness as measured by RRS.

**Methods**

In order to determine the extent to which captive ancestry biases estimates of RRS, we developed a forward-time, individual-based model (i.e., the model tracked individuals over time). Our model is both age and stage-structured and fully accounts for overlapping generations. As an exemplar species we used coho salmon, as this species is commonly bred in captivity and captive-born individuals are often released into the wild (semelparous, maximum lifespan = 7 years; Quinn 2005). Within this framework, we considered 2 scenarios: 1) a single 50-year supplementation period and 2) two 50-year supplementation periods separated by 25 years without supplementation (Figure 1). Here, we describe the model in terms of the steps that occurred within the wild population followed by those that occurred in the captive-breeding program.

Simulations were initiated with the wild population at carrying capacity (total census population size = 500). The model begins with reproduction in the wild, where we randomly paired individuals and then assigned the number of offspring per pair using a random deviate generated from a gamma distribution (shape = 0.5, rate = 0.5). A gamma distribution with these parameters was selected because it accurately characterizes the high variance in reproductive success of salmon spawning in wild populations (Seamons and Quinn 2010; Christie et al. 2014b). 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

\[
N_{t+1} = r \left(1 - \frac{N_t}{K}\right)
\]

where population size \(N_{t+1}\) was determined by the per capita growth rate \(r = 0.1\), carrying capacity \(K = 500\), and population size prior to reproduction \(N_t\). For each year in the model, we further modified this value using an estimate of density independent effects (e.g., climatic variables, etc.) using a random deviate from a

![Figure 1](https://academic.oup.com/jhered/article-abstract/108/5/583/3819408/fig1)
normal distribution with a mean equal to $N_{00}$ and standard deviation equal to model parameter $l$, where $l$ dictates the strength of density-independent processes ($l = 5$). 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 lifespan of the species. Because mortality was applied each year, the probability of any one individual being removed from the population scaled with that individual's age. Finally, we incremented surviving individuals’ age and stage (immature to mature) and, to mimic the semelparous life-history strategy employed by coho salmon, all spawning adults were removed from the model after reproduction.

After allowing for the age structure to stabilize over 75 years, we created and managed a supplementation program that released captive-born offspring into the wild population. Prior to reproduction in the wild, 15% of the wild-born adults were randomly selected for use as breeders in the captive population. Once in captivity, we randomly paired adults and released captive-born offspring back into the wild population at 1 year of age. As in the wild population, the reproductive success of each captive pair was determined with a random deviate from a gamma distribution (shape = 0.5, rate = 0.5). After producing offspring in the run-year for which they were selected, the captive breeders were removed from the model (i.e., new captive parents were used during each year of supplementation). The release of offspring from the captive breeding program was implemented under 2 scenarios (Figure 1). First, we implemented a captive-breeding and supplementation program that continued for 50 consecutive years (beginning in year 75). Second, we again initiated a 50-year supplementation program (beginning in year 75) but this was followed by a 25-year respite from supplementation and then by a second, 50-year supplementation program (beginning in year 150).

Prior to the start of the captive breeding program, all individuals were assumed to have no prior history of captive breeding. All wild-born offspring were assigned a fitness value as a random deviate from a normal distribution with the mean equal to the average parental fitness and the standard deviation equal to 0.005. This low standard deviation limits the amount of mutation and additive genetic variation, limiting a rapid recovery of the wild population after supplementation has ceased (i.e., we are assuming that the response to selection in captivity depletes the additive genetic variation). The fitness of captive-born offspring was modified by assigning a reduced fitness value, according to run parameters (fitness reduction range = 0–1; increments of 0.1). We assumed that all individuals born in captivity were subject to identical fitness reductions; all individuals born in captivity were assigned a fitness value equal to 1 minus the fitness reduction value of the particular simulation. We subsequently used the assigned, individual fitness values to apply a one-time survival cost; prior to reproduction, individuals were randomly selected to be removed from the population with a probability equal to the individual's fitness reduction. Thus, individuals with captive ancestry and lower fitness were more likely to be removed from the population than individuals that lacked captive ancestry.

To address the effects of supplementation on estimates of RRS, we compared estimates of RRS using the equation

$$\text{RRS} = \frac{W}{W_*}$$  \hspace{1cm} (2)

where the average fitness for captive-born individuals ($W$) is given relative to the average fitness of wild-born individuals ($W_*$); when all reproduction occurs in the wild (Araki and Blouin 2005). We calculated RRS by estimating the fitness of wild-born individuals in 2 ways: first, we calculated fitness of the wild-born individuals ($W_*$) from the supplemented, wild populations (RRS); second, we calculated the fitness of wild-born individuals without captive ancestry (RRS) by measuring the average fitness of individuals from control populations that did not have any captive ancestry (Figure 1). By dividing $W$ by these 2 different estimates of $W_*$ we could measure the difference in RRS estimates calculated with and without captive ancestry. We simulated 100 replicate populations for all parameter combinations considering both the scenario with a single supplementation period and the scenario with 2 supplementation periods. After the simulations were complete, we compared mean RRS to the true RRS, 5–50 years into each supplementation period for both of the supplementation scenarios we considered.

Results

We found that when captive ancestry is present in the wild population, RRS will nearly always be overestimated given sufficient time for introgression with captive-born individuals. For all RRS values tested, $\text{RRS}$ was approximately equal to RRS at the start of supplementation, since very few opportunities for captive-born individuals to reproduce in the wild had occurred (Figure 2a). However, this was not true in scenarios where supplementation occurred in a population with previous captive ancestry (Figure 2e). Furthermore, we found that $\text{RRS}$ was equal to RRS when RRS was exactly one or zero. This pattern occurred across all of the time points we sampled and for both the single and double supplementation scenarios (Figure 2).

The difference between $\text{RRS}$ and true RRS (i.e., bias) increased through time. As captive ancestry increased in the wild population, fitness in the wild population moved closer to the fitness values of captive-born individuals, resulting in $\text{RRS}$ estimates that trended towards one (Figure 2b–d). When supplementation occurred in a wild population that had previously been supplemented, the increase in $\text{RRS}$ occurred more quickly due to the higher proportion of individuals with captive ancestry already existing in the wild population (Figure 2e–h). Furthermore, the extent to which $\text{RRS}$ was upwardly biased was related to the speed at which captive ancestry increased in the wild population: the bias took the longest to increase when reproductive success of captive-born individuals was very low and was quickest when reproductive success of captive-born individuals in the wild was high.

Discussion

Overall, we found that when there is captive ancestry in a wild population that results in a heritable reduction in fitness, wild-born reproductive success is underestimated relative to what it would be if no captive-born individuals had been released. Because captive ancestry in the wild population increases through time, $\text{RRS}$ estimates obtained after only 5 years of population supplementation may already be upwardly biased. This phenomenon can only occur when captive-born individuals reproduce with wild-born individuals (i.e., there must be gene flow from captive to wild populations), meaning that supplementation programs that aim to release individuals that are similar to wild-born individuals are especially susceptible to calculating upwardly biased $\text{RRS}$ values. Supplementation programs targeted at populations that already have reduced fitness resulting from previous supplementation periods are also likely to have biased RRS estimates since the “wild” population starts out with a greater amount of captive ancestry [see Araki et al. (2007) for description of a population with two back-to-back supplementation programs].
There are 2 assumptions made explicit in our model that must also occur in nature for this bias in RRS to be observed. First, the reductions in fitness must be due to genetic adaptation to the captive environment (i.e., they must be due to a response to selection and they must be heritable). Changes in reproductive success that are transient, such as environmental or maternal effects, will not result in long-term changes to the fitness of wild individuals. We think this assumption is valid in light of increasing empirical evidence (Araki et al. 2009; Christie et al. 2016; Ford et al. 2016). Second, we assumed that there was limited additive genetic variation and mutation, such that there were not substantial increases in the fitness of wild individuals with captive ancestry after the supplementation ceased. Given the timescales we measured, we think this assumption is reasonable, but more empirical data on how quickly wild populations with captive ancestry could rebound is greatly needed.

One potential method for correcting the bias is to measure fitness of the wild population prior to the release of captive-born individuals. Under ideal conditions, pre-release fitness estimates should not contain any captive population ancestry and would provide an unbiased estimate of RRS. However, previous release of captive-born individuals in the population of interest may preclude this option (Figure 2e–h) and, if captive-supplementation history is unknown, reliance on a presupplementation fitness estimate may lead to unknowingly biased estimate of RRS. Furthermore, because both environmental conditions and fitness landscapes change over time, reproductive success estimates across different time periods may not be comparable and such a comparison may ultimately result in biased estimates of RRS of an unknown direction and magnitude (Lande 1985; Poelwijk et al. 2007). Therefore, using reproductive success estimates that were measured prior to supplementation may not be a sufficiently reliable method for correcting RRS bias.

Incorporating captive ancestry into estimates of fitness may be a viable method for correcting bias in RRS. Quantifying population ancestry could be accomplished using GWAS, pedigrees, or analysis of population admixture (Tang et al. 2010; Jarvis et al. 2012; Wollstein and Lao 2015), although a more nuanced understanding of the evolution that occurs in captivity would allow for a more targeted characterization approach (e.g., SNP genotyping). When applied to wild-born individuals of unknown pedigree, population ancestry could be used to quantify the proportion of the genome descended from the captive population. However, an unbiased estimate of RRS would require both an accurate and precise estimate of captive ancestry and the corresponding fitness tradeoffs. Thus, while we advocate use of fitness estimates corrected for captive ancestry, we encourage careful consideration of all the challenges associated with estimating captive ancestry when attempting to correct wild population fitness estimates.
Conclusions

Evaluating the population-wide impacts of supplementation is important in ensuring that supplementation efforts have a positive impact on wild populations. However, relying on estimates of wild-born fitness when captive ancestry is present in the wild population overestimates the relative fitness of captive-born individuals in the wild. Because this phenomenon has little to do with species biology, the same trend is likely to occur across a variety of taxa and habitats. Therefore, we suggest a careful interpretation of RRS, and other metrics that compare captive-born fitness to wild-born fitness, and suggest particular attention be paid to supplementation duration and history within each particular population.

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Data Availability

All model-based code is available in Dryad (doi: 10.5061/dryad.519d0).

References


