
Contributed Paper

Evaluating Alternative Strategies for Minimizing Unintended Fitness Consequences of Cultured Individuals on Wild Populations

MARISSA L. BASKETT* AND ROBIN S. WAPLES†

*Department of Environmental Science and Policy, University of California, Davis One Shields Avenue, Davis, CA 95616-5270, U.S.A.
email mlbaskett@ucdavis.edu

†Northwest Fisheries Science Center, National Marine Fisheries Service National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, U.S.A.

Abstract: *Artificial propagation strategies often incur selection in captivity that leads to traits that are maladaptive in the wild. For propagation programs focused on production rather than demographic contribution to wild populations, effects on wild populations can occur through unintentional escapement or the need to release individuals into natural environments for part of their life cycle. In this case, 2 alternative management strategies might reduce unintended fitness consequences on natural populations: (1) reduce selection in captivity as much as possible to reduce fitness load (keep them similar), or (2) breed a separate population to reduce captive-wild interactions as much as possible (make them different). We quantitatively evaluate these 2 strategies with a coupled demographic-genetic model based on Pacific salmon hatcheries that incorporates a variety of relevant processes and dynamics: selection in the hatchery relative to the wild, assortative mating based on the trait under selection, and different life cycle arrangements in terms of hatchery release, density dependence, natural selection, and reproduction. Model results indicate that, if natural selection only occurs between reproduction and captive release, the similar strategy performs better. However, if natural selection occurs between captive release and reproduction, the different and similar strategies present viable alternatives to reducing unintended fitness consequences because of the greater opportunity to purge maladaptive individuals. In this case, the appropriate approach depends on the feasibility of each strategy and the demographic goal (e.g., increasing natural abundance, or ensuring that a high proportion of natural spawners are naturally produced). In addition, the fitness effects of hatchery release are much greater if hatchery release occurs before (vs. after) density-dependent interactions. Given the logistical challenges to achieving both the similar and different strategies, evaluation of not just the preferred strategy but also the consequences of failing to achieve the desired target is critical.*

Keywords: artificial propagation, domestication selection, hatcheries, migration load, *Oncorhynchus* spp, quantitative genetic model, rapid evolution

Evaluación de Estrategias Alternativas para Minimizar las Consecuencias No Inesperadas en la Adecuación de Individuos Criados en Cautiverio sobre Poblaciones Silvestres

Resumen: *Las estrategias de propagación artificial a menudo incluyen selección en cautiverio que conduce a atributos que no son adaptativos en el medio silvestre. En programas de propagación enfocados a la producción en lugar de contribuciones demográficas a las poblaciones silvestres, los efectos sobre las poblaciones silvestres pueden ocurrir por medio de escapes no intencionales o la necesidad de liberar individuos en ambientes naturales durante parte de su ciclo de vida. Para reducir consecuencias no esperadas de la propagación artificial sobre poblaciones naturales, los manejadores pueden reducir la selección en cautiverio lo más posible para reducir la carga de adaptabilidad o criar una población separada para reducir, lo más posible, las interacciones cautiverio-medio silvestre. Evaluamos cuantitativamente estas estrategias de manejo con un modelo demográfico-genético que basamos en pesquerías de salmón del Pacífico. El modelo*

incorporó una variedad de procesos y dinámicas relevantes: selección en el criadero relativo al medio silvestre, apareamiento selectivo con base en el atributo seleccionado, y ordenamiento diferente de los eventos en el ciclo de vida (liberación del criadero, densodependencia, selección natural y reproducción). Cuando la selección natural ocurrió entre la reproducción y la liberación, la reducción de la selección en cautiverio fue más efectiva en la reducción de consecuencias no esperadas en la adecuación que la cría de una población separada. Sin embargo, cuando la selección natural ocurrió entre la liberación y la reproducción, ambas estrategias redujeron las consecuencias no esperadas en la adecuación por la oportunidad de la selección natural de purgar individuos no adaptativos antes de que ocurra el entrecruzamiento. En este caso, el método apropiado dependería de la factibilidad de cada estrategia y de la meta demográfica (e.g., incremento de la abundancia natural o asegurar que una alta proporción de reproductores naturales sea producida naturalmente). Los efectos sobre la adaptabilidad de la liberación de individuos criados en cautiverio fueron mucho mayores cuando la liberación ocurrió antes (versus después) de las interacciones densodependientes. Debido a los retos logísticos de reducir la selección en cautiverio y la cría de una población separada, la evaluación de la estrategia preferida y de las consecuencias de no alcanzar la meta deseada son de importancia crítica.

Palabras Clave: Carga de migración, criaderos, evolución rápida, modelo genético cuantitativo, *Oncorhynchus* spp., propagación artificial, selección de domesticación

Introduction

Artificial propagation can be both a conservation tool, in the case of captive breeding (Ebenhard 1995; Frankham et al. 2002), and a potential threat to biological diversity, in cases such as spillover or release from agriculture, forestry, ranching, and aquaculture leading to invasive species or types (Laikre et al. 2010). Selection in captivity, whether accidental or purposeful, often leads to traits that are maladaptive in the wild (Frankham et al. 2002). In captive breeding focused on conservation-based supplementation, such selection is widespread and can undermine the success of the program by leading to poor survivorship or reproductive success of artificially-propagated individuals and degrading fitness in wild populations (Ebenhard 1995; Frankham 2008). In artificial propagation programs focused on production, such selection can lead to unintended negative fitness effects on wild populations when any artificially-propagated individuals escape (Laikre et al. 2010).

Escapement (i.e., release of artificially propagated individuals into the natural environment) might occur through unintentional spillover (e.g., from agriculture and commercial forestry) or when program goals depend on releasing individuals into the natural environment for part of their life cycle (e.g., hatcheries for marine stock enhancement, game bird supplementation, insect pollinators). Production programs are responsible for the majority of released individuals (Laikre et al. 2010), but their fitness effects on natural populations have received less attention in wildlife and forestry management. Although containment would avoid fitness consequences by ensuring that no cultured individuals have an opportunity to interbreed with wild individuals, complete containment is nearly impossible to achieve, and many production programs necessarily involve the intentional release of cultured individuals to the natural environment.

For reducing unintended fitness consequences in the context of captive breeding, the goal is clear: avoid as much selection in captivity as is feasible (Frankham et al. 2002). Reducing selection in captivity is also a potential strategy for reducing unintended fitness consequences in production programs, but the fact that such programs do not have demographic contribution to wild populations as part of their goals suggests a second alternative: purposefully selecting for different phenotypes to separate them from the wild population. Under the latter strategy, not only might the lower fitness of captive-reared individuals lead to a low likelihood of survival in the wild, but if any traits under selection (e.g., timing of reproduction, body size) affect assortative mating, then captive-reared and wild individuals might be less likely to interbreed.

In the first, “similar” strategy, interbreeding events will have small fitness effects but will be common, whereas in the second, “different” strategy, interbreeding events will be rare but any that do happen will have large fitness effects. Therefore, these alternatives trade-off between their effect on (1) the probability that captive-bred individuals will survive in the wild and successfully reproduce, and (2) the severity of the genetic consequences from each interbreeding event that does occur. This trade-off is inevitable given that heritable attributes that reduce survival or reproductive success of cultured individuals will also lead to the most serious reductions in fitness for interbreeding events that occur. Although these inherent trade-offs have been recognized by some (Naish et al. 2007), no detailed evaluations have been conducted.

Salmon hatcheries present a study system that encapsulates both types of artificial propagation programs (conservation hatcheries for wild population support, production hatcheries for fishery support; Utter & Epifanio 2002; Naish et al. 2007) and for which negative fitness effects of selection in captivity on a variety of traits are well-established (Reisenbichler & Rubin 1999; Araki

et al. 2008; Hutchings & Fraser 2008). Hatcheries involve partial-life-cycle captive rearing, taking in adults during their return migration, or the migration of adults from oceans to the river spawning grounds, and releasing the offspring before outmigration, or the migration of juveniles from rivers to the ocean feeding grounds. Therefore, hatchery-reared and wild fish inevitably interact at some stages.

Here we rigorously test the intuitive logic of the similar and different strategies through a quantitative model, with the goal of determining whether one strategy performs better (i.e., has lower unintended fitness consequences on the wild population) in general and, if not, identifying the conditions under which each is more effective at reducing unintended fitness consequences on wild populations. A number of models applied to selection in hatchery or aquaculture environments (e.g., Hutchings 1991; Lynch & O'Hely 2001; Tufto 2001; Ford 2002) provide insight into elements of this question, especially the influence of the amount of exchange between the captive and natural population. We provide the first integration of all of the dynamics relevant to the similar and different alternatives, where both survivorship and mating likelihood depend on trait differences driven by selection, into a single model.

Methods

We base the model on a generic Pacific salmon (*Oncorhynchus* spp.) life cycle with coupled demographic and genetic dynamics, where the evolutionary dynamics represent a generic trait. One example of a relevant trait is spawn time, a heritable trait under selection in hatcheries (Hoffnagle et al. 2008) that affects both fitness and assortative mating (i.e., fish spawning around the same time are more likely to mate with each other; Hendry & Day 2005). From the coupled dynamics, we analyze how fitness and demographic effects of the hatchery depend on model assumptions with respect to life cycle timing and density dependence.

Conceptual Model Overview

The model follows the coupled demographic-genetic dynamics through 4 major stages: reproduction, outmigration, ocean residence, and return migration (Fig. 1), with census at the spawner stage just before reproduction. We use a quantitative genetic model such that phenotypes can assume a continuum of values depending on both the underlying genotypes and random environmental effects. During reproduction, genotypes are inherited and phenotypes depend on genotypes. We model assortative mating with a correlation between phenotypes of individuals in a mating pair (i.e., 2 individuals with more similar phenotypes are more likely to mate) to account for the

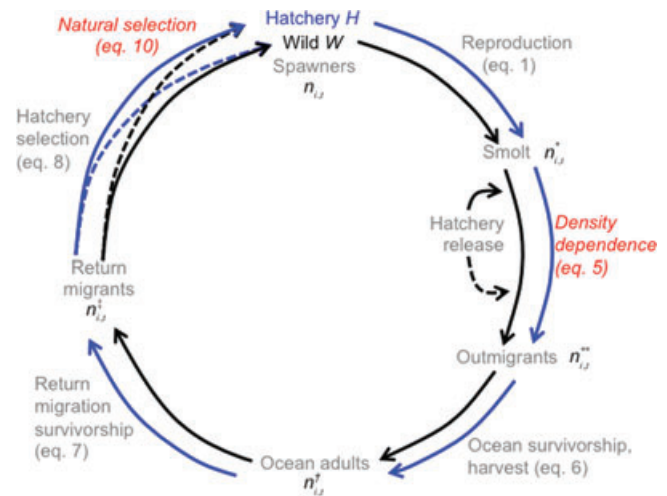


Figure 1. Illustration of model dynamics (Eqs. 1–10). Each time step represents a full life cycle. Within each time step, the model steps through reproduction, hatchery release, density-dependent mortality, ocean survivorship and harvest, return migration survivorship, and both hatchery and natural selection. Both density-dependence and natural selection, highlighted in red and with italics, can occur at either outmigration or return migration, where the 5 orderings explored are, (1) as illustrated, which serves as the default life cycle; (2) both density dependence and natural selection on return migration, with density dependence preceding selection; and, given natural selection on outmigration, (3) density dependence on outmigration before natural selection; (4) density dependence on outmigration after natural selection; or (5) density dependence on return migration. Under the default life cycle, we explore hatchery release after (dashed arrow) as well as before (solid arrow, the default) density dependence. The black dashed line between return migration and spawning indicates any wild fish selected for the hatchery, and the blue dashed line between return migration and spawning indicates hatchery fish escapement to spawn in the wild.

effect of phenotypic selection in the hatchery on mating likelihood with wild individuals. We assume that per-capita production of juveniles is higher in the hatchery than in the wild, which is essential for any successful hatchery program (Waples et al. 2007).

During outmigration, both hatchery release and density-dependent mortality occur, with the relative timing of these events determining whether hatchery and wild fish affect each other's survivorship. During ocean residence, we implement density-independent mortality to model both natural and harvest survivorship. During return migration, 3 events occur: return migration survivorship, hatchery removal, and natural selection. For return

migration survivorship, we assume lower survivorship for hatchery-reared fish due to the non-genetic effects of rearing in the hatchery environment (as hatchery fish generally have lower smolt-adult survival than wild fish; Waples et al. 2007).

We assume that the hatchery selects on the phenotype during collection of hatchery broodstock; for example, hatcheries often select early returning fish to ensure they meet their egg-take quotas (Hoffnagle et al. 2008). How much the optimal trait in the hatchery differs from that in the wild determines where the hatchery strategy falls on the different-similar continuum. Here we model a hatchery that selects only on phenotype and does not distinguish wild-reared and hatchery-reared fish, and anything not selected for the hatchery can spawn in the wild. For natural selection, we implement stabilizing selection for an optimal trait, which determines the survivorship of natural spawners of both wild and hatchery origin. In

function $P(f|g)$. Then, given per-capita reproductive output (smolts per spawner) R_i in location i (where $R_W < R_H$), the offspring population density distribution in each location i at time t is

$$n_{i,t}^*(f, g) = R_i N_{i,t} P(f|g) \iiint T(g|g_1, g_2) \times \Psi_i(f_1, g_1, f_2, g_2) df_1 dg_1 df_2 dg_2 \quad (1)$$

(analogous to Slatkin 1970). To define the mating function, we let assortative mating depend on parental phenotypes (f_1, f_2) and the correlation between successful mating phenotypes a_i ($0 \leq a_i < 1$, where $a_i = 0$ for no assortative mating; note that any assortment by population of origin can only occur due to phenotypic differences). In this case, following Feldman & Cavalli-Sforza (1977, Eq. 16), the mating function is the encounter probability (product of proportion of each parental type in the population) weighted by the correlation factor according to

$$\Psi_i(f_1, g_1, f_2, g_2) = \frac{\phi_{i,t}(f_1, g_1)}{\int \phi_{i,t}(f_1, g) dg} \frac{\phi_{i,t}(f_2, g_2)}{\int \phi_{i,t}(f_2, g) dg} \exp \left[-\frac{(\phi_{i,t}(f_1, g_1) - \mu_{f,i,t})^2 - 2a_i(\phi_{i,t}(f_1, g_1) - \mu_{f,i,t})(\phi_{i,t}(f_2, g_2) - \mu_{f,i,t}) + (\phi_{i,t}(f_2, g_2) - \mu_{f,i,t})^2}{2F_{i,t}(1 - a_i^2)} \right] \frac{1}{2\pi F_{i,t} \sqrt{1 - a_i^2}}, \quad (2)$$

reality, both natural selection and density dependence occur at a variety of life history stages. Therefore, we test alternative timings for these dynamics.

Mathematical Model Details

Our model follows the population density distribution $n_{i,t}(f, g)$, where $n_{i,t}(f, g) df dg$ describes the number of individuals in population i (W for wild or H for hatchery) at time t with phenotypes between f and $f + df$ and genotypes between g and $g + dg$. Integrating this distribution over all phenotypes and genotypes yields total population size $N_{i,t} = \iint n_{i,t}(f, g) df dg$, and normalizing this distribution yields joint genotype-phenotype probability distribution $\phi_{i,t}(f, g) = n_{i,t}(f, g)/N_{i,t}$. Because the dynamics considered here (in particular, disruptive selection by hatchery removal on the remaining population and the combination between populations experiencing different selection) can lead to substantial departures from normality of both breeding values and environmental effects, we follow this full breeding value distribution (analogous to Coulson et al. 2010).

For reproduction, given 2 individuals with phenotype-genotype combinations (f_1, g_1) and (f_2, g_2) , let their mating probability density be $\Psi(f_1, g_1, f_2, g_2)$, the probability density of their offspring genotypes depend on parental genotypes given the transmission function $T(g|g_1, g_2)$, and the probability density of their offspring phenotypes depend on offspring genotypes given the

given mean phenotype $\mu_{f,i,t} = \iint f \phi_{i,t}(f, g) df dg$ and phenotypic variance $F_{i,t} = \iint (f - \mu_{f,i,t})^2 \phi_{i,t}(f, g) df dg$. Given each offspring genotype drawn from a distribution determined by the average of its parental genotypes and the amount that mutation increases genetic variance each generation M , the transmission function is

$$T(g|g_1, g_2) = \frac{1}{\sqrt{2\pi(G_{i,t}/2 + M)}} e^{-\frac{(g - \frac{g_1 + g_2}{2})^2}{G_{i,t}/2 + M}}. \quad (3)$$

This approach assumes a large number of loci each contribute additively, with a small effect of each locus, to the overall genotype. Note that the genetic variance used for the offspring distribution (population-level variance $G_{i,t} = \iint (g - \mu_{g,i,t})^2 \phi_{i,t}(f, g) df dg$ given mean genotype $\mu_{g,i,t} = \iint g \phi_{i,t}(f, g) df dg$) ignores linkage disequilibrium to account for the effect of evolving genetic variance on inheritance and follow the full reproductive model from our source for the assortative mating dynamics (Feldman & Cavalli-Sforza 1977); changing this assumption does not affect the qualitative trends presented here (Appendix S1). Finally, given random environmental variation E and no phenotype plasticity, the offspring phenotype is randomly distributed around its genotype according to

$$P(f|g) = \frac{1}{\sqrt{2\pi E}} e^{-\frac{(f - g)^2}{2E}}. \quad (4)$$

During outmigration, we employ density-dependence according to the Beverton-Holt function with parameter α (a widely used model of density dependence in salmon

dynamics, especially stage-specific density dependence, e.g., Scheuerell et al. 2006; see Satake & Araki 2012 for how choice of density dependence can affect results in hatchery models). Given hatchery release before density-dependence, this yields

$$n_{i,t}^{**}(f, g) = \frac{n_{i,t}^*(f, g)}{1 + \alpha \sum_{j \in \{W, H\}} \iint n_{j,t}^*(f', g') df' dg'} \\ = \frac{n_{i,t}^*(f, g)}{1 + \alpha \sum_{j \in \{W, H\}} N_{j,t}^*}. \quad (5)$$

During ocean residency, density-independent survivorship occurs with proportion v_o surviving, which combines both natural and harvest mortality. The surviving population is

$$n_{i,t}^{\dagger}(f, g) = v_o n_{i,t}^{**}(f, g). \quad (6)$$

During return migration, each population experiences population-dependent return survival $v_{s,i}$, where $v_{s,W} = 1$ and $v_{s,H} < 1$ to express the post-smolt survivorship and spawning success of hatchery-reared fish relative to that of wild-origin fish, where hatchery-reared fish generally have lower survival and spawning success due to non-genetic effects of hatchery rearing. Therefore, each return-migrating population is

$$n_{i,t}^{\ddagger}(f, g) = v_{s,i} n_{i,t}^{\dagger}(f, g). \quad (7)$$

Note that applying lower density-independent survivorship for hatchery-reared fish to earlier life history stages (ocean stage, at outmigration after density dependence) will result in the same outcome for the population distribution dynamics.

Next the hatchery removes individuals for hatchery spawning, in the process selecting on the phenotype. The hatchery selects for optimal trait θ_H given selection variability S_H , which is inversely related to selection strength. We modify this selection by the proportion $\rho_{H,t}$ controlled by the target hatchery population size, such that the hatchery population density in the next generation is

$$n_{H,t+1}(f, g) = \rho_{H,t} \exp \left[-\frac{(f - \theta_H)^2}{2S_H} \right] \\ \times (n_{W,t}^{\ddagger}(f, g) + n_{H,t}^{\ddagger}(f, g)). \quad (8)$$

To determine the modifier $\rho_{H,t}$, we set a target of \hat{N}_H fish for hatchery rearing and a maximum proportion of the total spawning population that can be removed for the hatchery ρ_M such that

$$\rho_{H,t} = \min \left(\frac{\hat{N}_H}{\sum_{i \in \{W, H\}} \iint \exp \left[-\frac{(f - \theta_H)^2}{2S_H} \right] n_{i,t}^{\ddagger}(f, g) df dg}, \rho_M \right). \quad (9)$$

The remainder not selected for the hatchery return to spawn in the wild, undergoing natural selection. This selection occurs as stabilizing selection for the optimal trait θ_W given selection variability S_W inversely related to selection strength (as in Lande 1976; Ford 2002). Applying this selection to the wild-spawning population yields

$$n_{W,t+1}(f, g) = \exp \left[-\frac{(f - \theta_W)^2}{2S_W} \right] \\ \times \left(1 - \rho_{H,t} \exp \left[-\frac{(f - \theta_H)^2}{2S_H} \right] \right) \\ \times (n_{W,t}^{\ddagger}(f, g) + n_{H,t}^{\ddagger}(f, g)). \quad (10)$$

Note that because the same trait determines both assortative mating (Eq. 2) and fitness (Eq. 10), this model falls under the magic trait class of models concerning assortative mating (Gavrilets 2004).

In addition to the sequence of events described above, we explore the model with hatchery release after density dependence (Eq. 5 without the summation), density dependence (Eq. 5) at spawning rather than outmigration (after hatchery selection, to model competition for spawning sites), and natural selection (Eq. 10) occurring after reproduction (before hatchery release, with density dependence on outmigration before or after natural selection or on return migration).

Model Implementation and Analysis

Because the model is not analytically tractable, we numerically simulate the relevant scenarios. We choose values (e.g., strong natural selection as reflected in values of S_W and S_H ; all values provided in Table 1) where fitness effects of hatchery-reared fish influence the population dynamics of wild fish, as it is under those circumstances that the question of similar versus different hatchery strategies is of most interest. Because hatchery environments can incur both artificial selection, which is often stronger than natural selection, and weaker, relaxed selection for traits under selection in the wild, we use a default of equivalent selection strength in the hatchery to the wild. For the hatchery production (R_H) and relative hatchery survivorship in the wild ($v_{s,H}$, reflective of non-genetic effects of rearing in the hatchery environment), we choose values in line with empirical observation of the overall returning number of adults per spawner (Waples et al. 2007). In addition, we choose a default environmental variance (E) to result in a heritability similar to values observed for life history and phenological traits (Carlson & Seamons 2008); note that heritability evolves as genetic variation evolves with the evolution of the full breeding value distribution. We choose the value for the amount that mutation increases genetic variation (M) relative to the environmental variance from the

Table 1. Model parameters, meaning, and default values used in the numerical analysis of Eqs. (1)–(10).

Parameter	Description	Default value
R_i	Per-capita reproductive output (smolts per spawner) in each of the hatchery and wild populations	$R_W = 3; R_H = 8R_W$
a_i	Phenotypic correlation between mating pairs (strength of assortative mating)	$a_W = a_H = 0.5$
M	Amount mutation increases genetic variance each generation	10^{-3}
E	Environmental variance	1
θ_i	Optimal trait in environment i (wild or hatchery)	$\theta_W = 50, \theta_H = 35 - 50$
S_i	Width of selection function in environment i (inversely related to selection strength)	$S_H = S_W = 5$
α	Density-dependent parameter for Beverton–Holt function	3×10^{-5}
ν_o	Ocean survivorship (density-independent)	0.7
$\nu_{s,H}$	Relative smolt-to-adult survivorship and spawning success for hatchery-reared fish (given $\nu_{s,W} = 1$)	0.3
\hat{N}_H	Target population size for the hatchery	1000
ρ_M	Maximum proportion of the total population (or wild population in the case of a mixed-target hatchery) that the hatchery can remove	0.8

empirically-observed range reported in Lynch (1988). We also explore model sensitivity to all parameter values.

We initialize the model at the expected equilibrium for each population considered independently (natural population size at its carrying capacity based on the density-dependence parameter α , hatchery population size at hatchery capacity \hat{N}_H , genotype-phenotype distribution centered the optimal traits for each environment). Then we run the model for 50 time steps (generations), which is beyond the point where simulations reach equilibrium, and report equilibrium censused in the spawning stage. For more details on the numerical analysis, see Appendix S1.

We use 3 metrics to determine the fitness and demographic effects of the hatchery on the wild population. The first metric is the equilibrium fitness of wild individuals in the natural (wild) environment $\bar{F}_{W,W}$. To determine fitness of population i in environment j , we use the population's genotype-phenotype probability distribution $\phi_{i,t}(f, g) = n_{i,t}(f, g)/N_i$ multiplied by the environment-dependent fitness for each phenotype $\exp[-(f - \theta_j)^2/(2S_j)]$ and integrated over all phenotypes and genotypes

$$\mathcal{F}_{ij,t} = \iint \exp\left[-\frac{(f - \theta_j)^2}{2S_j}\right] \phi_{i,t}(f, g) df dg \quad (11)$$

(Lande 1976). The second metric is the equilibrium wild population size ($\bar{N}_W = \iint \bar{n}_W(f, g) df dg$, where the bar indicates equilibrium value), scaled by the equilibrium population size in equivalent simulations without a hatchery ("no-hatchery baseline"). Both of these metrics are derived from the full phenotype-genotypic population density $\bar{n}_W(f, g)$; see Appendix S2 for sample results that describe this distribution at equilibrium. Third, to explore the effect of the hatchery on the wild population in the same way that it is often measured empirically,

we calculate the fraction of natural spawners that are of natural origin (i.e., the proportion of natural spawners $n_{W,t+1}$ in Eq. 10 that originated in the wild as $n_{W,t}^*$ fry, thus measured on the within-generation, individual level rather than the genetic level). These metrics reflect a goal of minimizing unintended consequences given a production program, rather than a captive breeding program focused on demographic supplementation, as the similar versus different question applies only to the former.

Our central determinant for the degree of similarity of selection in the hatchery and natural environments is the difference in optimal traits θ_H and θ_W . Assuming constant θ_W while changing $\theta_H \leq \theta_W$, $\theta_H - \theta_W = 0$ indicates identical hatchery and natural environments (as a theoretical benchmark unlikely to be achieved in reality), and decreasing $\theta_H - \theta_W$ indicates increasing difference in selection between the 2 environments. Given the underlying dynamics, larger values for the optimal trait in the hatchery relative than in the wild ($\theta_H - \theta_W > 0$) would lead to a mirror image to these plots. We express hatchery selection in terms of the value of $\theta_H - \theta_W$ rather than in terms of phenotypic standard deviations because, with genetic and phenotypic variance evolving with the full breeding value distribution, these values change with θ_H (Appendix S2).

Results

When investigating a variety of options for the timing of density dependence and natural selection (Fig. 2) in the life cycle, we find that whether the different strategy presents a viable alternative to the similar strategy depends critically on the timing of natural selection. If natural selection only occurs after reproduction, before

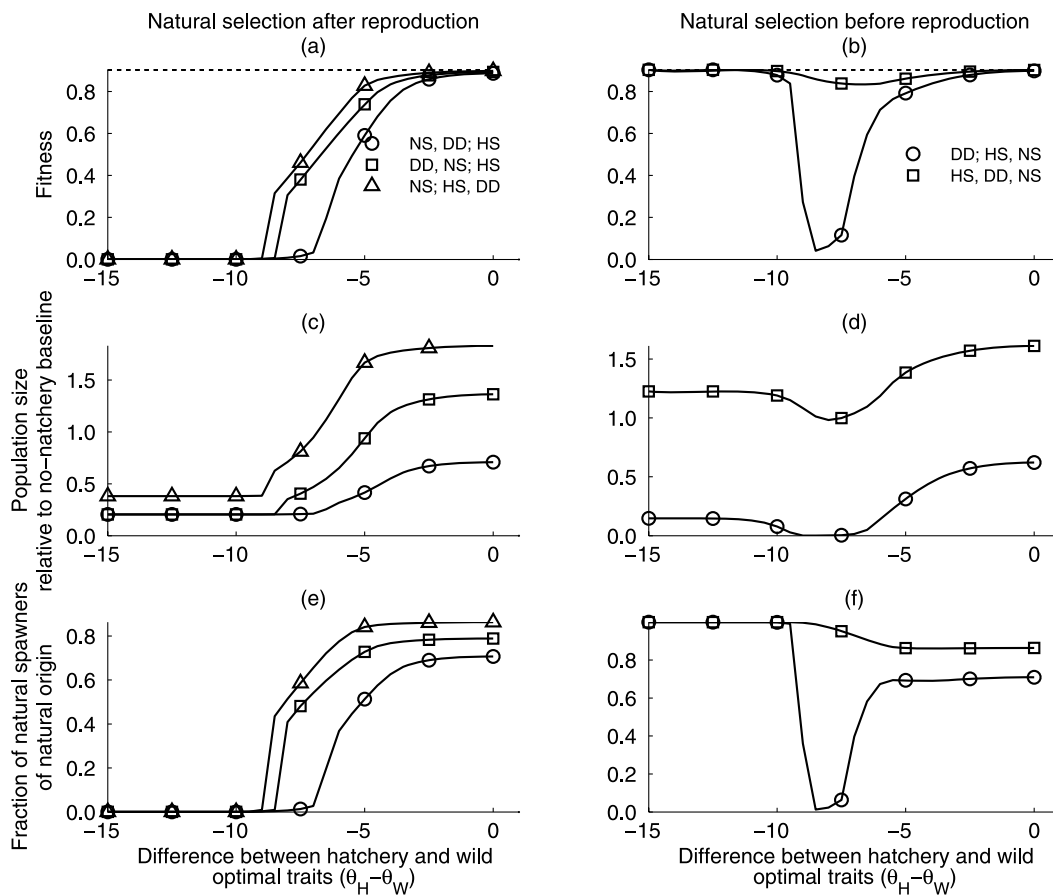


Figure 2. The effect of different timings for natural selection (NS), density-dependence (DD), and hatchery removal/selection (HS). The semicolon in the legends separates events that occur at outmigration from those that occur at return migration; all 3 events in the lines with squares in the right-hand column occur after return migration. Columns separate simulations with natural selection occurring at outmigration (panels a, c, e) or return migration (panels b, d, f), and rows provide the model outcome for 3 different metrics of hatchery effects on wild population (fitness of wild individuals in the natural environment in panels a and b, wild population size scaled to the population size at equilibrium for the equivalent model without a hatchery in panels c and d and fraction of natural spawners of natural origin in panels e and f). The dotted line in the fitness plots indicates the equilibrium value in equivalent simulations without a hatchery (below one because of mutation-selection balance plus environmental variance leads to phenotypic variation around the optimal phenotype). Delimiting markers (circles, squares, and triangles) indicate every fifth data point.

hatchery release, then hatchery-reared fish not taken into the hatchery will spawn in the wild before natural selection can remove their genes, and their offspring present a continual, recurring fitness drag, which increases with increasing difference between the hatchery and wild selection (lower value for $\theta_H - \theta_W$ in Fig. 2a). This leads to a decline in the wild population size (Fig. 2c) and replacement of the wild population by fish of hatchery origin (Fig. 2e). On the other hand, if natural selection occurs just before or at spawning, and if hatchery-reared fish are different enough that most will not survive that natural selection event, most wild spawners will be of wild origin (Fig. 2f) and have the same fitness as if there were no hatchery (Fig. 2b). In other words, the different

(low $\theta_H - \theta_W$) strategy is a viable alternative to the similar ($\theta_H - \theta_W \sim 0$) strategy only when natural selection occurs between release and reproduction. When there is an intermediate fitness minimum between these 2 strategies, both extremes tend to perform equivalently in terms of fitness effects on the wild population (Fig. 2b), and the demographic effect depends on the metric: keeping them similar tends to lead to greater natural population sizes (Fig. 2d) but a lower fraction of natural spawners of natural origin (Fig. 2f) compared to making them different.

When exploring the relative timing of hatchery release and density-dependent mortality in the wild (with natural selection during return migration; Fig. 3), we find a strong interaction between density-dependent

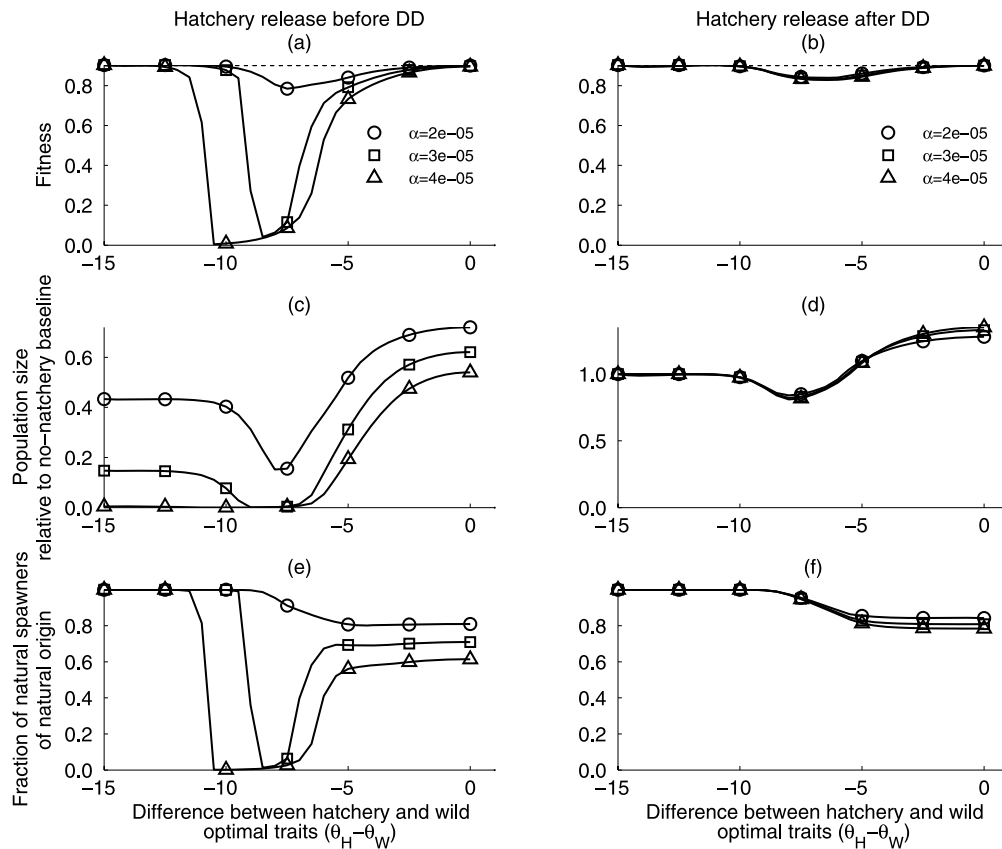


Figure 3. The effect of different assumptions for the density-dependent dynamics: hatchery-reared fish release before (left column; panels a, c, e) or after (right column; panels b, d, f) density-dependent mortality occurs in the wild, for differing strengths of density-dependence (increasing strength, or decreasing carrying capacity, with increasing Beverton-Holt parameter α). The dotted lines in the fitness plots indicate the no-hatchery baseline.

and fitness effects of hatchery-reared fish on the wild population. Specifically, intermediate hatchery selection (such that hatchery-reared fish are similar enough for some to survive to reproduce in the natural environment but different enough to cause a significant fitness drag when they do so) has a much more negative effect, both in terms of population size and fitness, when hatchery-reared fish are released before density dependence (Figs. 3a, c, e as compared to Figs. 3b, d, f). In this case, hatchery-reared fish first increase the density-dependent mortality of natural spawners at outmigration and then reduce the fitness of the remaining wild population at spawning, as opposed to only affecting fitness.

The qualitative trend of both similar and different strategies minimizing unintended fitness consequences in comparison to an intermediate strategy if natural selection occurs between outmigration and return migration applies to a wide array of parameter values (Fig. 4). The potential for significant fitness consequences of an intermediate strategy depends most strongly on the values for the strength of density dependence, the reproductive output both for natural spawners and in the hatchery, ocean survivorship, and the hatchery size.

Discussion

Keep them Similar versus Make them Different

Our model indicates that, for artificial propagation programs where escapement is unintentional, the effect of domestication selection on wild populations and the appropriate strategies for mitigating unintended fitness consequences depends critically on the relative timing of natural selection, density dependence, and release of artificially propagated individuals in the life cycle. Specifically, the different strategy of breeding a separate population is a viable alternative to the similar strategy of reducing selection in the captive environment only if strong natural selection occurs between captive release and reproduction, so that it can purge maladapted individuals before they leave any offspring (Fig. 2b). Otherwise, if natural selection only occurs between reproduction and captive release, the different strategy leads to a migrational meltdown (*sensu* Ronce & Kirkpatrick 2001), where input of maladaptive individuals reduces survivorship the following generation and hence increase the relative contribution of the maladaptive individuals

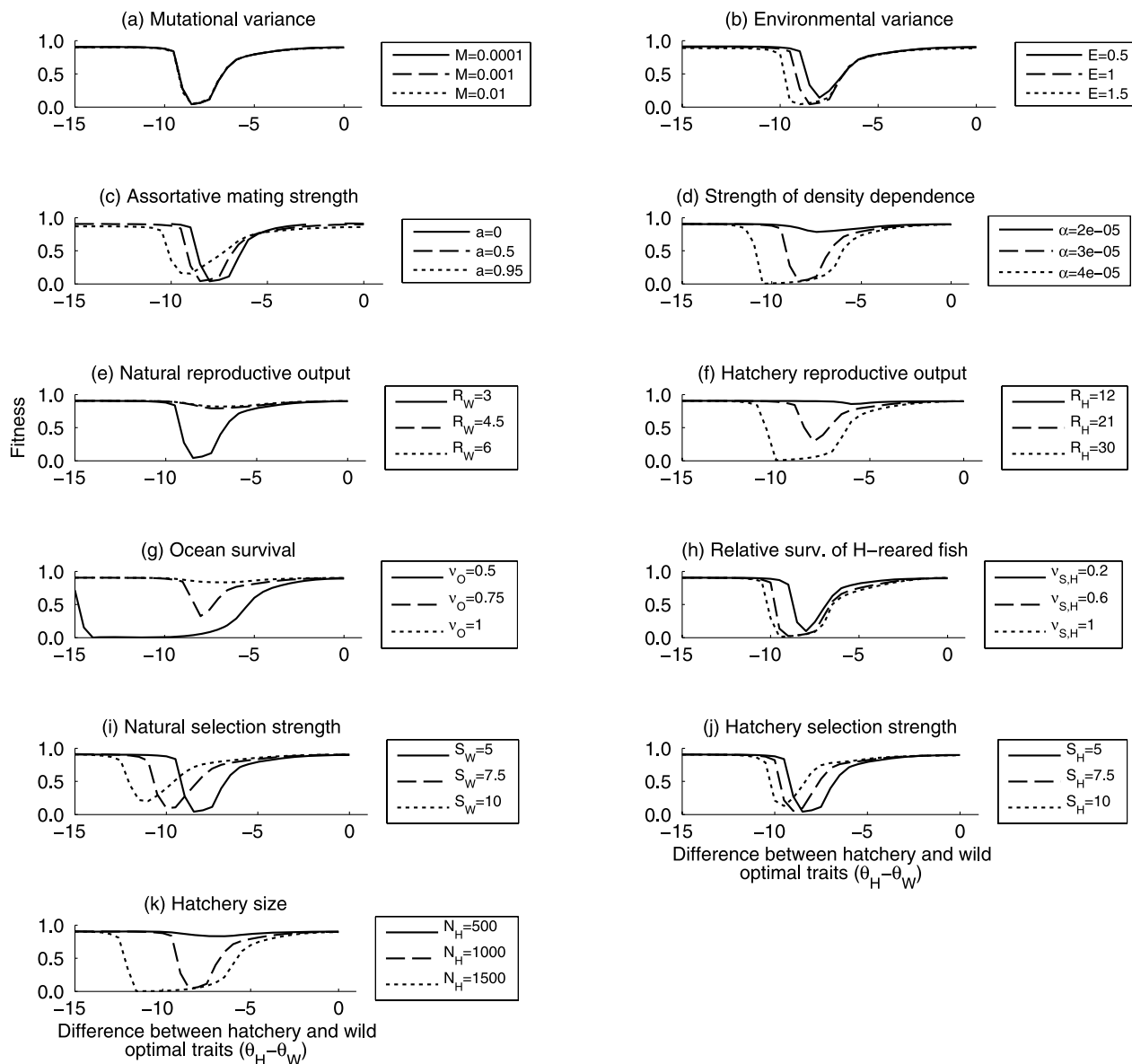


Figure 4. The effect of different parameter values on the model outcome under model default assumptions (density dependence at outmigration, hatchery release before density dependence, and natural selection at spawning) on fitness of wild fish in the wild. In panel (e), $R_H = 8R_W$ for all simulations. Note that the carrying capacity decreases with increasing α (strength of density dependence) in panel (d) and S_i is inversely related to selection strength in panels (i)–(j).

from the captive population each generation, with the eventual replacement of the wild population with genotypes adapted to the captive environment. In this case, the similar strategy always performs better (Fig. 2a).

Our results resonate with a variety of existing models. Replacement with maladapted individuals occurs in models with simpler genetic structure applied to aquaculture and crop production as well as hatcheries (Hutchings 1991; Byrne et al. 1992; Haygood et al. 2003; Satake & Araki 2012) in addition to generic models of gene flow and spatially variable selection (reviewed by Lenormand

2002). Purging of maladapted individuals also occurs in a model with one-way migration (J. Huisman and J. Tufto unpubl.), where selection occurs between migration and reproduction, given strong selection. In addition, informed by a model without explicit genetic dynamics, Lorenzen (2005) argues that the greatest negative effects of stock enhancement on the wild population will occur at intermediate fitness differences. Finally, Ronce & Kirkpatrick (2001) highlight the importance of the relative timing of migration, selection, and reproduction in their generic model, where selection between migration

and reproduction decreases the potential for migrational meltdown.

Parallels between our results and this wide-ranging set of models strengthen the generality of our conclusions, which expand on previous results to provide a more comprehensive comparison of the similar and different strategies. Furthermore, though our model construction is motivated by salmon, the use of multiple life cycle constructs and a generic stabilizing selection function allows for broad applicability for artificial propagation programs that involve partial-life-cycle captive rearing (e.g., other fish hatcheries, game birds, insect pollinators). In particular, our central conclusion that strong natural selection between captive release and reproduction is necessary for the different strategy to be a viable alternative to the similar strategy (robust to a wide variety of parameter values; Fig. 4) can apply to the wide range of artificial production programs that exist across agriculture, forestry, hunting, and harvest (Laikre et al. 2010).

Under conditions where the similar and different strategies are viable alternatives for reducing unintended fitness consequences, the preferable strategy depends on both the demographic goal and relative feasibility of achieving each strategy. We discuss feasibility in the next section below. With respect to the demographic goal, the different strategy better achieves the goal of maximizing the fraction of natural breeders of natural origin due to the purging effect (Fig. 2f). Conversely, the similar strategy better achieves the goal of maximizing wild population size due to the potential for the similar, captive-reared individuals to contribute to the population with relatively minor fitness drag (Fig. 2d).

A Question of Feasibility

Our simulations and the relevant theory thus support the possibility of the different and similar strategies as viable alternatives, provided they are extreme enough, with intermediate strategies leading to the greatest fitness and demographic consequences. However, extremes of either strategy can be difficult or impossible to achieve in reality. Effectiveness of the similar strategy will be constrained by the difficulty in minimizing domestication selection in the benign captive environment (Frankham et al. 2002). Given that multiple traits under varying degrees of management control are under selection in captive environments (Reisenbichler & Rubin 1999; Hutchings & Fraser 2008) and drive fitness consequences for wild populations (Araki et al. 2007), the use of a single trait is a limiting assumption of our model; however, Tufto (2010) found that the inclusion of multiple co-evolving traits with correlated selection has a relative minor effect in an analogous model.

Genetic or life history constraints can also limit how different of a trait a captive environment can select for,

in particular whether it can be extreme enough to avoid interbreeding and fitness consequences (Seamons et al. in press). Furthermore, achieving the different strategy with a naive population would typically incur substantial transient fitness consequences. Specifically, because a strategy different enough to reduce unintended fitness consequences requires selecting for traits that lead to a very low likelihood of survival in the wild, the frequency of such traits in a naive natural population will be extremely low. Therefore, a naive wild population will not have enough individuals to initially fill the target numbers for a new captive population with an extreme different strategy, and that captive population will only be able to arrive at the different strategy through gradual directional selection (rather than the instantaneous stabilizing selection modeled here given the equilibrium analysis). In this case, the population would move through a phase of large unintended fitness consequences (the fitness trough in Fig. 2b) before it becomes different enough for purifying selection to be effective. Avoiding this transient phase of large fitness consequences would require either controlling the escapement of captive-reared individuals during the period of directional selection or starting with a pre-adapted captive population (e.g., from a different location).

Therefore, though our model suggests the best possible scenario for either strategy, it also indicates the potential for substantial fitness and demographic consequences for artificial propagation programs that do not achieve these ideals, in line with the fitness effects suggested in previous models of selection in hatchery and aquaculture environments (e.g., Lynch & O'Hely 2001; Tufto 2001; Ford 2002). These models indicate that additional policies can improve both the similar and different strategies. Specifically, targeting a combination of captive-reared and wild-reared fish in a hatchery can slow down domestication selection and therefore assist the similar strategy (Lynch & O'Hely 2001; Ford 2002), and controlling captive-to-wild gene flow can help isolate the artificially propagated population and therefore assist the different strategy (Hutchings 1991; Lynch & O'Hely 2001; Tufto 2001; Ford 2002).

Because of both logistical challenges to achieving these various controls as well as the potential for unexpected outcomes, evaluating the outcome under optimal control as well as the consequences of deviation from the management target is critical. Models such as ours provide quantitative frameworks for such evaluations. For example, the rate of change in fitness for deviations from the extreme strategies (absolute slope at either side of the fitness trough) can indicate which strategy will incur greater fitness consequences for failure to achieve the desired target, which is typically the different strategy under the parameter values explored here (Fig. 4).

The Role of Density Dependence

In addition to the timing of natural selection, we find that the timing of density dependence relative to captive release has a significant influence on potential for unintended fitness consequences of artificial propagation (Fig. 3). In particular, much stronger fitness and demographic consequences occur with captive release before as compared to after density-dependent interactions because in the former case captive-reared fish increase the density-dependent mortality of wild individuals, thus reducing their relative contribution to the next generation. The timing of population regulation relative to exchange (soft vs. hard selection) has long been established as a major determining factor in the effect of exchange between populations experiencing differential selection (Christiansen 1975).

In reality for salmon, density dependence occurs at a variety of stages, and the strength of density dependence can vary with environmental conditions. Therefore, one expects any negative hatchery effects on wild populations to be particularly strong during years with greater resource limitation, such as years with poor ocean conditions for outmigrating salmon (Levin et al. 2001). One possible management implication of our results is that later hatchery release, which would reduce the amount of density-dependent interactions between hatchery-reared and naturally spawned fish, would also reduce unintended fitness consequences. A more generic model of genetic exchange between 2 populations, where density dependence occurs both before and after exchange, suggests that the efficacy of such an approach will depend critically on the relative size of each (here, hatchery vs. wild) population (Debarre & Gandon 2011). However, increased time in captivity will increase the opportunity for domestication. Furthermore, later hatchery release can also increase straying of hatchery-reared fish due to the loss of imprinting on the habitat at early stages, which might degrade metapopulation structure and diversity, with the potential to reduce resilience to environmental change (Lindley et al. 2009). Therefore, metapopulation structure and environmental heterogeneity, 2 processes not included here, require consideration for a more conclusive recommendation with respect to release timing.

Model Assumptions

As with any model, ours necessarily includes a number of simplifying assumptions. The theory of gene flow provides insight into how these assumptions might affect our results. Along with the assumptions discussed above, we implement a quantitative genetic model that ignores linkage disequilibrium, drift, and overlapping generations. Though overlapping generations would not affect the outcome of our model given the lack of environmental variation in many cases, they would affect cases where

domestication selection affects generation time, such as by selecting for earlier maturity. Existing theory indicates that exchange between populations and any subsequent fitness load can cause similar demographic consequences in models with and without overlapping generations (Tufto 2000).

Genetic drift can lead to the accumulation of deleterious alleles, which can interact with selection in captivity to drive unintended fitness consequences (Lynch & O'Hely 2001). On the other hand, drift can also allow for a positive role of exchange between populations through the replenishment of lost genetic variation (Alleaume-Benharira et al. 2006). Therefore, it is not clear that ignoring genetic drift biases our model in any given direction. Typically, incorporating a finite number of loci contributing to a trait with linkage and variation in the effect size of individual loci does not substantially influence the outcome of models with exchange between populations experiencing differential selection (Tufto 2000; Huisman & Tufto *in press*). However, the effect of these assumptions does become stronger with strong selection and large differences between populations, which occurs under the different scenario here. One assumption typical to quantitative genetic models that we carefully avoid is that of normal genetic and phenotypic distributions: we follow full breeding value distributions, which we found necessary to properly evaluate the different strategy (Appendix S1). Overall, whereas relaxation of these assumptions might be necessary for a tactical model applied to a particular scenario, the general conclusions from our strategic model (*sensu* May 2001) highlight the crucial importance of the relative timing of natural selection, reproduction, density dependence, and captive escapement to understanding and quantifying the effect of captive rearing on wild populations.

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Supporting Information

A more detailed description of the numerical analysis implementation (Appendix S1) and sample output of the full genotype-phenotype distributions (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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