

# Relaxed selection and environmental change decrease reintroduction success in simulated populations

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## Keywords

individual-based simulation; phenotypic variation; conservation; behaviour; captive populations; environmental change.

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## Abstract

Previous work has shown that captive environments can relax selective pressures on various traits, resulting in significantly more trait variance in captive-bred versus wild populations. This increased variance could be one cause of the high mortality rates observed when captive-bred populations are released into the wild, because a significant proportion of the released population exhibits traits that are no longer adapted to the wild. Here we use evolutionary simulation to examine the effects of relaxed selection on trait variance and population persistence when populations are reintroduced into static and changing environments. Our simulations show that when wild environments remained stable and selective pressures on given traits were quite strong (1) relaxation of selective pressures led to significant increases in trait variance; (2) trait variance rapidly decreased when pressures were restored; (3) the smaller the population size, the lower the probability of persistence; and (4) there was often a significant lag time between reintroduction and eventual extinction, reinforcing the importance of long-term monitoring after release. When captive-bred populations were reintroduced into changing environments, strength of selection in the release habitat was the factor that most influenced survivorship. Amount of change between the source and release habitat and the population's carrying capacity also influenced survivorship, but to a lesser extent.

## Introduction

Conservation biologists know that more diverse populations have more evolutionary potential and may thus be better equipped to respond to environmental change than less diverse populations (Frankel & Soulé, 1981; Holt & Gomulkiewicz, 2004). Diversity also provides a buffer against forces such as genetic drift and inbreeding depression that can quickly erode a small population's viability. Maximizing diversity, however, does not always lessen risk of extinction (Lande & Shannon, 1996) – in some cases, high trait variance can be too much of a good thing.

Captive populations are often extremely small and management decisions are rooted in the goal of maintaining genetic diversity. These populations, however, are exposed to selective pressures that shape phenotypes and genotypes that are adaptive for the captive environment (Archer, 1973; Frankham *et al.*, 1986, 2000; Hedrick, 1992; Allendorf, 1993; Arnold, 1995; Price, 1998; McPhee & Carlstead, 2010). Over generations, these pressures can alter trait distribution and expression, thus making captive populations distinct from their wild counterparts (McPhee, 2004a,b).

The increased variance associated with relaxed selection occurs when a selective force is removed from or lessened

in the environment. A prime example is lack of predator pressures for island (Blumstein, 2002; Beauchamp, 2004; Blumstein & Daniel, 2005) and captive species (Heath *et al.*, 2003; Bremner-Harrison, Prodohl & Elwood, 2004; Håkansson & Jensen, 2004). In a conservation context, such an increase in trait variance can affect how populations fare upon reintroduction to the wild (McPhee & Silverman, 2004; McPhee, 2004a). If trait variance is higher in a captive-bred than a wild population, a greater proportion of the population will exhibit traits in the tails of the distributions – traits that are possibly selected against (or at least not selected for) in the wild (McPhee & Silverman, 2004). Given this, understanding how population-level patterns of phenotypic trait expression affect population persistence is vital to understanding how populations will respond to rapid changes in their environment, whether that change is transfer to a captive environment, transfer to the wild from captivity, or anthropogenic changes in the wild.

To get a longer-term perspective on how such changes can affect population persistence, we simulated shifts in trait expression on a fitness landscape as a function of altered selective pressures. We wanted to know how release from and restoration of selective pressures, populations size and environmental change would affect trait distribution and population persistence. We were particularly interested in

shifts experienced by wild populations moving into captivity and then being reintroduced into the wild.

## Methods

We used an individual-based model with panmictic breeding, and this section summarizes four major components of our model: (1) phases representing presence or absence of selective pressures on a given trait; (2) sequence of events representing a generation; (3) steps in generating offspring from parents; and (4) how we simulated the effects of different levels of selection and environmental change. A more detailed description of the methods is provided in our electronic supporting information (Supporting Information Appendix S1).

We simulated populations with varying carrying capacities ( $K = 20, 50, 100, 200$ ) across three phases with different selective pressures: (1) a 30-generation *initial phase* (IP<sub>1-30</sub>; ‘wild’) with stabilizing selection pressure on the two traits being modelled; (2) 20 generations in a *relaxed selection phase* (RX<sub>1-20</sub>; ‘captive’) where selective pressures on the modelled traits were removed; and (3) 20 generations in a *restored selection phase* (RST<sub>1-20</sub>; ‘reintroduction’) where, once again, pressures pushed traits to a common central point (Supporting Information Appendix S1, section 1). We realize that these phases correspond only loosely to complexities of true wild, captive, and reintroduction environments. These ideas, however, were important motivating factors in this work and provide useful ways of thinking about our model.

For the initial and RSTs we modelled a simple fitness landscape as a 2-D surface, where the two axes represented two traits ( $x$  and  $y$ ), and the surface height ( $w$ ) represented fitness of an individual having those two trait values (Fig. 1). In the RX, there was no fitness peak; that is all individuals had the same base fitness regardless of their trait values.

The standard deviation of the peak ( $\sigma$ ) was either 50 (strong selection on the given trait), 100 (moderate selec-

tion) or 200 (weak selection). In the Restored Phase, we either maintained the Initial Phase peak location or simulated environmental change ( $m$ ) by shifting the peak an equal number of units along the  $x$  and  $y$  axes.

In all phases, we modelled a generation with the following sequence of steps:

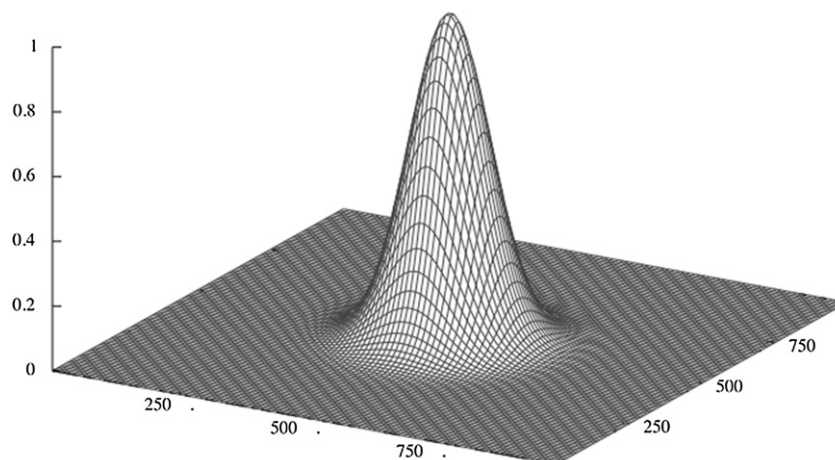
1. Run a mortality pass where each individual has a chance to be culled based on their fitness.
2. While the number of individuals in a given generation ( $N$ ) is greater than carrying capacity  $K$ , repeatedly draw individuals at random from the population and subject them to the culling process.
3. Randomly pair remaining individuals. (Note: parents have no sex so pairing is truly random).
4. For each pair, generate four offspring:
  - a. Perform crossover on the two parents.
  - b. Mutate resulting offspring.
  - c. Compute fitness of offspring.
  - d. Compute an inbreeding penalty based on the parents’ similarity.
  - e. Compute final, penalized fitness of offspring.

For each pair of parents this sequence of recombination, mutation, penalty computation and fitness calculation was repeated four times to generate four offspring.

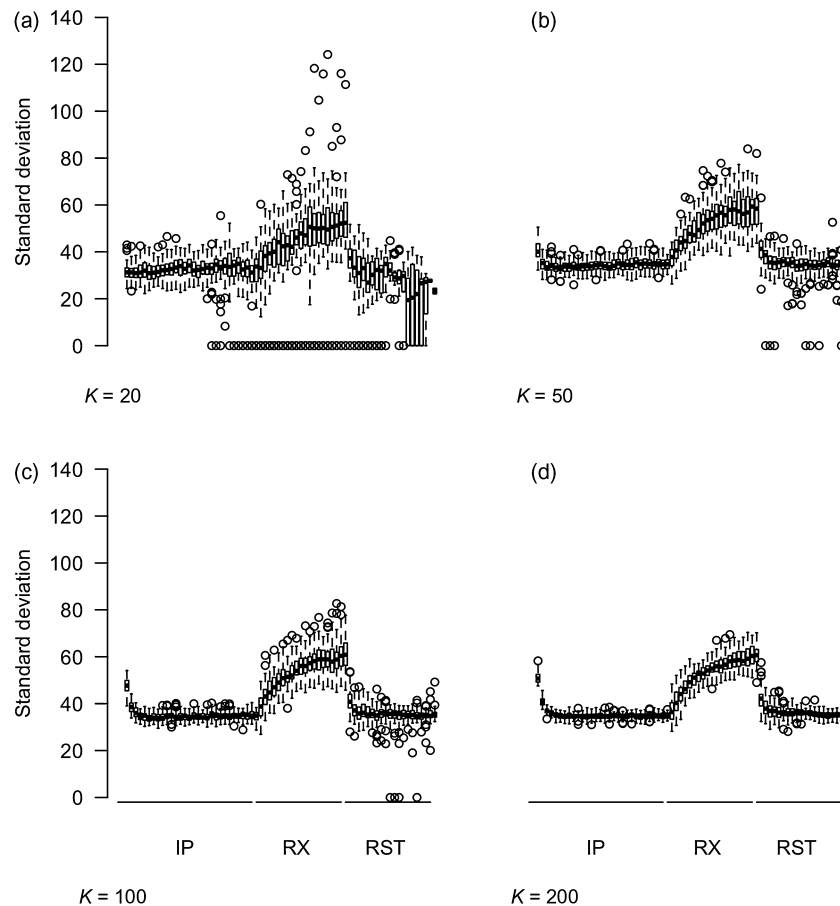
5. If the generation is moving into a new phase, randomly select founders for the next phase.

To run a mortality pass, we generated a random number drawn uniformly from  $[0, 1]$  for each individual. If that number was greater than their (penalized) fitness, then they were culled from the population. This meant that individuals with relatively high fitness were less likely to die than those with relatively low fitness values. Individuals that survived the mortality pass then reproduced.

The fitness of an individual having trait values  $x$  and  $y$  was the height of the surface ( $w$ ) at point  $(x, y)$ . In all three phases, however, this basic fitness was modified by an inbreeding penalty that penalized similarity between parents (Supporting Information Appendix S1, section 6). For detailed descriptions of individual representation, offspring



**Figure 1** The fitness landscape used in the initial phase and the restored selection phase of our runs. The fitness surface is a 2-D Gaussian centred at (500, 500) with standard deviation 50 in both dimensions, scaled so the peak has height 0.95.



**Figure 2** Boxplots of standard deviation for trait  $x$  across all generations for the four groups:  $K =$  (a) 20; (b) 50; (c) 100; and (d) 200. Number of runs for all groups is 50, although runs decrease as generations increase because some go extinct. The initial phase is generations  $IP_1$  to  $IP_{30}$ , the relaxed phase is generations  $RX_1$  to  $RX_{20}$ , and the restored phase is generations  $RST_1$  to  $RST_{20}$ . IP, initial phase; RST, restored selection phase; RX, relaxed selection phase.

generation, inbreeding penalty and mutation, please see the Supporting Information Appendix S1.

For each generation across all three phases (IP, RX, RST), we ran 50 independent trials for each combination of values for carrying capacity ( $K$ ; [20, 50, 100, 200]), peak width ( $w$ ; [50, 100, 200]), and peak movement ( $m$ ; [0, 75, 150]). We then measured various properties of these runs, including changes in population size and trait variance over time. The contribution of each parameter to survivorship after reintroduction was analysed with regression trees (rpart package in R, R Development Core Team, 2008). All statistical analyses were done in R (R Development Core Team, 2008).

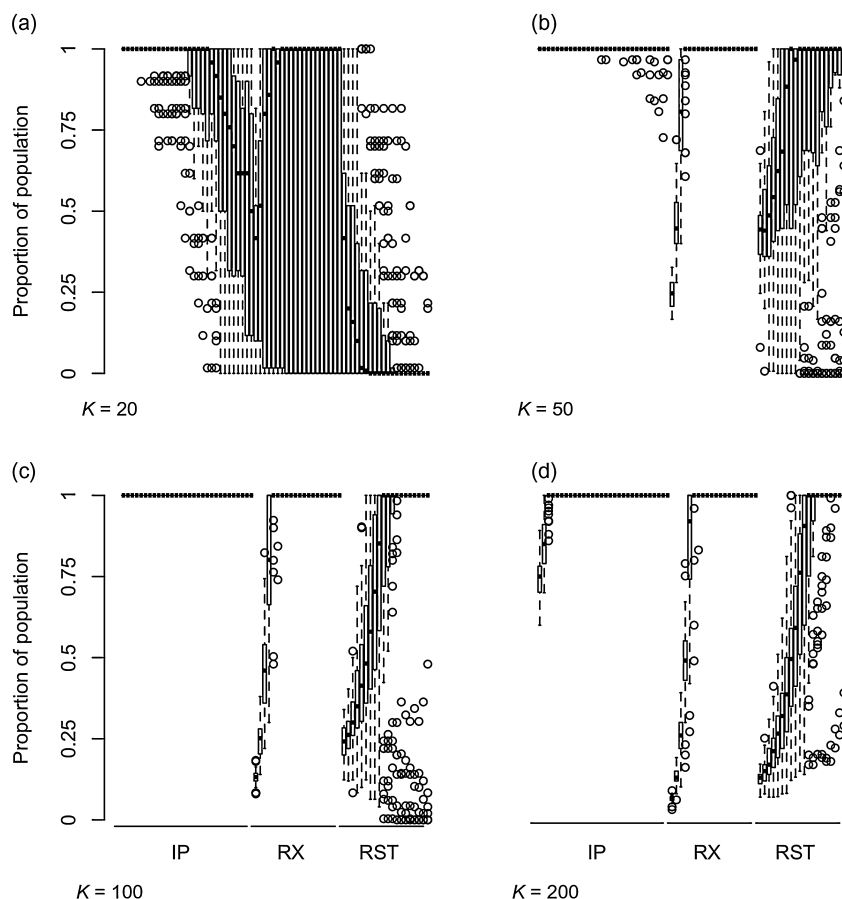
## Results

### Effects of relaxed selection on trait variance and population size

In all four groups ( $K = 200, 100, 50, 20$ ) with peak width  $\sigma = 50$  (strong selection) and no movement ( $m = 0$ ; no environmental

change), variance around  $x$  and  $y$  increased drastically in the RX and decreased again at restoration of selection. In addition, as  $K$  got smaller fluctuations in population size increased. Figure 2 summarizes the data for all 50 runs at a given generation (each generation is summarized as a boxplot). This graph clearly indicates the magnitude of change observed within and across groups. All reported patterns are virtually identical for both traits so we only present results for  $x$ . In addition, for the purposes of this study, 'extinction' requires the final individual in the population to die. In reality, a species is extinct when it reaches only one sex remaining, no matter how many individuals. In addition, due to Allee effects, many species have extinction thresholds that are well above a single male and a single female.

Upon establishment of our initial populations ( $IP_{1-30}$ ), population sizes remained stable at  $K$  for groups  $K = 100$  and 200 (Fig. 3a,b). Population sizes for the  $K = 50$  group hovered at or just under  $K$  throughout the IP (Fig. 3c) while population sizes for  $K = 20$  steadily decreased (Fig. 3d). In the RX ( $RX_{1-20}$ ), all groups except  $K = 20$  stabilized at carrying capacity (Fig. 3d).



**Figure 3** Boxplots of the proportion of the population that survived over generation for all groups (50 runs):  $K =$  (a) 20; (b) 50; (c) 100; and (d) 200 across all phases. The initial phase is generations  $IP_1$  to  $IP_{30}$ , the relaxed phase is generations  $RX_1$  to  $RX_{20}$ , which was founded with 20 individuals, and the restored phase is generations  $RST_1$  to  $RST_{20}$ . IP, initial phase; RST, restored selection phase; RX, relaxed selection phase.

When selection was relaxed, variance increased rapidly in all four groups (Fig. 2) and the rise in variance was sharpest with larger  $K$ s. Upon restoration of selection ( $RST_{1-20}$ ), variance dropped immediately in all groups (Fig. 2). With the  $K = 200$  group, mean standard deviation dropped 64% in one generation (Fig. 2a). Restoration of selection not only decreased variance, but reduced population size for all groups. Mean population size dropped by 17, 21 and 22% for  $K = 200$ , 100 and 50, respectively, when selection was restored at generation  $RST_1$  (Fig. 3); for all groups, population sizes rebounded quickly. By the simulation's end (generation  $RST_{20}$ ), however, not all runs in the  $K = 50$  group had reached carrying capacity, but mean population size had increased to 49 (Fig. 3c).

The most dramatic effect of restoration of selection on population size was seen in  $K = 20$ . Unlike other groups,  $K = 20$  had runs in the RX that did not reach  $K$  and therefore, when selection was restored, there were fewer populations and within each there was rapid die off (Fig. 3d). Mean population size (of surviving populations) went from 20 to 12 in one generation, a 40% decrease. In 39 of 45 runs, the  $K = 20$  population went extinct by the end of the restoration

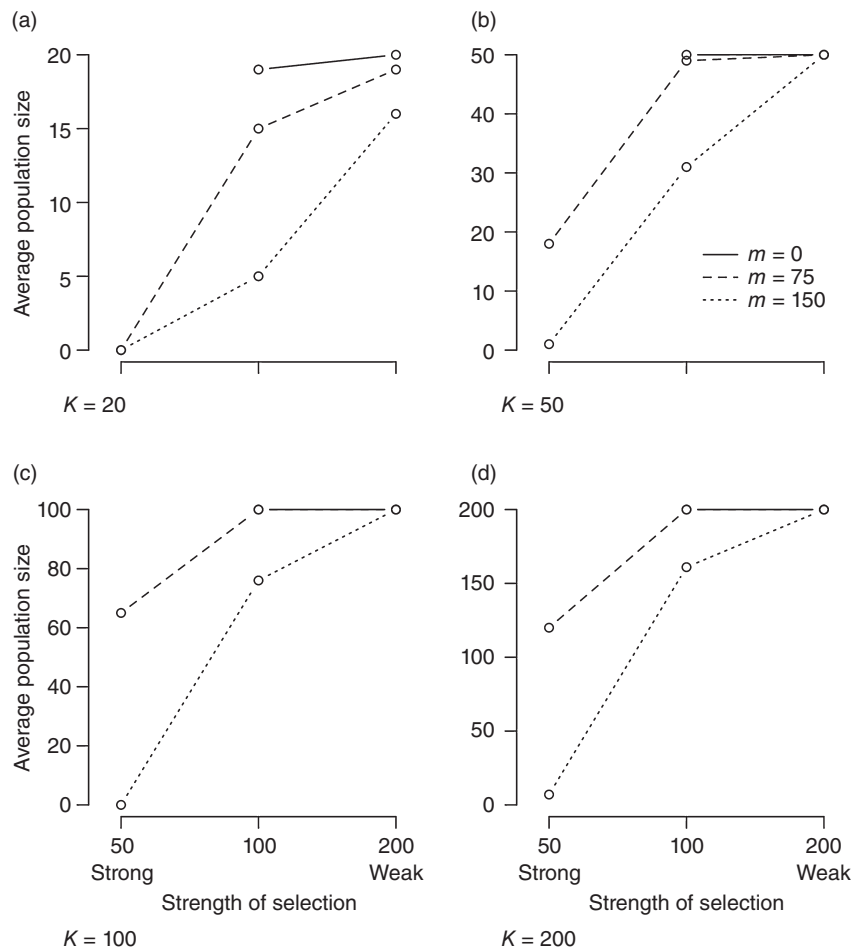
phase. Among the populations that died off by the end of the restoration phase, extinction was not necessarily immediate; in some cases, median population size did not reach zero until nine generations after reintroduction ( $RST_9$ ).

### Effects of environmental change and variable selective pressure

When environmental characteristics were held constant,  $K$  was the most important factor determining population persistence. However, we also wanted to understand the relative significance of carrying capacity, peak movement and the strength of selection on survival after reintroduction.

Partitioning the data with a regression tree showed that strength of selection (i.e. peak width,  $\sigma$ ) was the most important factor determining survivorship after reintroduction into the wild. The second most important factor was peak movement ( $m$ ); carrying capacity ( $K$ ) was least important (Fig. 4).

Reintroductions with the highest probability of persistence were those in which the wild environment exerted fairly weak selection ( $\sigma = 100, 200$ ) on the two traits and where



**Figure 4** Per cent of runs that had gone extinct 20 generations after release [restored selection phase (RST)<sub>20</sub>] as a function of environmental change (peak movement,  $m$ ), strength of selection (peak width,  $\sigma$ ), and carrying capacity ( $K$ ); solid lines  $m = 0$  (no change), dashed lines  $m = 75$ , and dotted lines  $m = 150$ .

there was little or no environmental change ( $m = 0, 75$ ). In these simulations, average population size was 98% of  $K$  at RST<sub>20</sub>. If there was weak selection ( $\sigma = 100, 200$ ) and significant environmental change ( $m = 150$ ), the weaker the selection, the more successful the reintroduction ( $\sigma = 200$ ,  $n = 95\%$  of  $K$ ). If  $\sigma = 100$  and  $m = 150$  (i.e. moderate selection and significant environmental change), populations with larger  $K$ -values did better than populations for which  $K = 20$ . For  $K = 50, 100$  and  $200$  average population sizes were 73% of  $K$ , but for  $K = 20$ , population sizes were only 23% of  $K$ .

In contrast, if wild selection pressures were strong ( $\sigma = 50$ ), populations were much less likely to survive. Small populations ( $K = 20$ ) were unable to persist when strong selection was coupled with any environmental change ( $m = 0, 75, 150$ ; average  $N = 0.7\%$  of  $K$ ) and regardless of  $K$ , populations had low probabilities of persistence when strong selection was coupled with significant environmental change ( $m = 150$ ; average  $N = 1.3\%$  of  $K$ ).

The most likely to survive reintroduction into an environment with strong selective pressures were larger populations ( $K > 20$ ) released into a static environment ( $m = 0$ ; average

$N = 89\%$  of  $K$ ). Larger populations ( $K > 20$ ) released into a changing environment ( $m = 75, 150$ ) showed moderate levels of persistence (average  $N = 54\%$  of  $K$ ).

## Discussion

We simulated release from and restoration of selective pressures on populations of various sizes in static and changing environments and analysed how such changes affected trait distribution and population persistence. These changes approximate shifts experienced by wild populations moving into captivity and then being reintroduced into the wild. Other researchers have used similar techniques to model genetics (Robert, 2009), but ours is one of the first to use evolutionary simulation to look at population response to reintroduction into stable and changing environments. Our simulations showed that when wild environments remained stable and selective pressures on given traits were quite strong, (1) relaxation of selective pressures led to significant increases in trait variance; (2) trait variance rapidly decreased when pressures were restored; (3) the smaller

the population size, the lower the probability of persistence; and (4) there was often a significant lag time between reintroduction and eventual extinction. When captive-bred populations were reintroduced into altered environments, the factor that most influenced survivorship was strength of selection in the release habitat. The amount of change between the source and release habitat and the population's carrying capacity also influenced survivorship, but to a lesser extent.

Overall, this work makes four major contributions: it demonstrates the importance of (1) considering the effects of variance on the success of conservation efforts that use captive-bred animals; (2) assessing any differences between the original wild habitat and the release habitat prior to reintroduction; (3) long-term monitoring after reintroduction; and (4) understanding how changing parameter values can affect projections of population persistence.

## Variance

Geneticists have long focused on maintaining variance in small populations. Conservation biologists measuring changes in behaviour and morphology, however, have only recently focused on within-population variance versus mean trait expression and how variation can affect reintroduction success.

Our simulations support the fundamental idea that, when selective pressures are relaxed, trait variance increases (Endler, 1986; McPhee, 2004a,b). Striking was how fast trait variance increased under relaxed selection in all of our groups. This is consistent with the idea that changes in selection can elicit significant responses within the first few generations after a population has been established – and these changes can persist over many generations (Arnold, 1995). Such a rapid increase in variance upon relaxation of selection suggests that, depending on the captive environment, populations, only a few generations removed from the wild are likely to have broader trait distributions than wild populations. Therefore, even populations that are brought into captivity for a relatively brief time can have substantially more individuals in the tails of the distribution than their wild counterparts.

Even more remarkable than the speed of increase upon relaxation of selection pressure was the speed of decrease in variance when pressures were restored. No matter how large the initial population, the captive-bred population suffered increased mortality upon release – suggesting that animals in the tails of the distribution are no longer adapted to survival in the release environment. For example, McPhee (2004a) demonstrated significantly increased variability in predator response behaviours because of relaxed selection over 14 generations in captive-bred oldfield mice (*Peromyscus polionotus*). Håkansson & Jensen (2004) show marked differences between different captive populations of junglefowl (*Gallus gallus*), reinforcing the idea that captive environments shape behaviour and morphology and increase variability in captive-bred populations. Bremner-Harrison *et al.* (2004) found variation in boldness and shyness within

a captive-bred population of swift fox (*Vulpes velox*). Upon release, animals categorized as bold died sooner than those categorized as shy.

Based on their findings, Bremner-Harrison *et al.* (2004) suggest that incorporation of behavioural variation in determining release animals should enhance the success of reintroduction programmes. This could occur in a number of ways. First, prior to release, animals could undergo behavioural testing to determine which individuals are most suited for the wild. This strategy, however, requires that the captive population be large enough that choices between individuals can be made, the animals are testable, and the animals are tested for behaviours relevant to survival in the wild. For many programmes, these requirements are difficult if not impossible to meet. Second, individuals slated for release can be trained in certain vital behaviours (van Heezik, Seddon & Maloney, 1999; Beck *et al.*, 2002), but this poses many of the same problems associated with testing and assumes that the necessary behaviours are learned and plastic. Third, reintroduction biologists can use the release ratio – a calculation that determines the appropriate size of a release population based on observed changes in variance between wild and captive populations (McPhee & Silverman, 2004). Like the other methods, this requires a sufficiently large captive population.

McDougall *et al.* (2006) and Watters & Meehan (2007) argue that providing pre-release environments that increase behavioural variation and maintain a range of temperaments within a captive population will increase success of conservation efforts. This argument, however, is based on the need to maintain natural selection regimes to avoid loss of variation and potential domestication of the captive population. In reality, we must strike a balance; there needs to be enough variance to allow for adaptation, but not so much that a significant proportion of the population is in fact maladapted to the release environment.

## Release habitat

Not only can species change over time in captivity, their habitat of origin can also change. If these changes are not considered when choosing a release site, the failure of a reintroduction can be all but guaranteed. The importance of habitat evaluation prior to reintroduction has been discussed elegantly by several authors (Cook *et al.*, 2010; Seddon, 2010; Osborne & Seddon, *in press*) and our work emphasizes the importance of assessing any differences between the original wild habitat and release habitat. Our simulations show that characteristics of the release habitat – strength of selection and amount of change from the original – have a greater impact on reintroduction success than does population size (though small populations suffer in all scenarios). The variable with the most important impact on survivorship after reintroduction is the strength of selection exerted on a given trait in the release habitat. For a population to survive reintroduction into a habitat with very strong selective pressures, the population needs to be large and/or there has been little environmental change (i.e. no

peak movement) between the source and release habitat. If the population is reintroduced into a habitat with weak selection on the trait in question, the population can withstand some peak movement regardless of  $K$ . If there is considerable movement, however, a population under strong selection will experience high mortality.

Although these characteristics are difficult to measure directly, proxies can be used. Strength of selection (peak width) could be measured in terms of variation and diversity of important variables within the habitat. For example, does the level of prey diversity favour a generalist or a specialist predator? Change between initial and release habitats is easier to measure, especially if before/after data exist on traits such as average temperature, habitat diversity, and abundance and diversity of predators (native and introduced).

### Monitoring

The third major contribution of these simulations is to reinforce the importance of long-term monitoring after reintroduction. In our simulations, small populations suffered high mortality rates upon restoration of selection with the majority of populations going extinct by nine generations after reintroduction. Nine generations, however, is a long time for a population to survive under initially novel conditions. Monitoring has been actively advocated as an essential part of any reintroduction (Kleiman, 1989; Seddon, Armstrong & Maloney, 2007), and the lag time before extinction seen here suggests that long-term monitoring is vital to accurately assess a programme's success. For long-lived species, this nine-generation window could mean that years of population monitoring will be required to determine whether or not the population has successfully established.

### Changing parameters

We designed the models to reveal broad patterns, not to be predictive for a specific species or habitat type. Thus, as with most models, a few of our parameter choices (e.g. mutation rates and inbreeding penalties) were somewhat arbitrary. Altering those choices, however, appears to lead to quantitative changes in the results, but not qualitative changes. General trends are preserved, while the specific slopes and magnitudes in plots like those in Fig. 2 may somewhat vary. For example, increasing the mutation rate or inbreeding penalty will increase the speed with which the variation increases, while decreasing will slow down that process. These shifts indicate that if vital rates change in the generations following reintroduction because of selection, the rates we assumed at reintroduction will not necessarily persist over time. This makes projecting population response after a reintroduction difficult and emphasizes the importance of using a good theoretical framework in reintroduction planning as well as the need for long-term monitoring.

As with any model, these simulations are limited because of their simplicity as compared with natural systems.

Therefore, a number of factors must be considered when interpreting these results.

First, these simulations assume only one introduction. Reintroduction programmes can have multiple releases of captive-bred individuals from various sources. Second, our simulated populations were exposed to selective pressures that acted only on two independent traits. In reality, selection acts on a multitude of traits, many of which are linked and/or epistatic. In addition, not all traits are equally susceptible to relaxed selection.

Third, our fitness landscapes are extremely simple and all individuals had equal fitness; the only differential source of mortality was the inbreeding penalty. In reality, all captive animals are not equally fit – the captive environment probably flattens the fitness landscape for some traits, shifts the peak for others, and even creates entirely new landscapes with multiple peaks. Our model is an oversimplification of the physical situation, but still provides meaningful insight into changes that occur in captivity without making too many arbitrary assumptions about captive conditions.

Fourth, we did not allow for any plasticity in trait expression. Once an animal's trait value was defined, it was fixed. Plasticity, however, can strongly influence an animal's ability to survive rapid environmental change (Price, Qvarnström & Irwin, 2003; Yeh & Price, 2004). Most importantly, however, these results support, and are supported by, field results (e.g. see Arnold, 1995; McPhee, 2004a) that suggest that variance can change quite quickly in response to significant changes in selection pressures.

Finally, our work did not address the effects of fragmentation or migration. In a review of strategies to minimize the genetic adaptation of animals to captivity, Williams and Hoffman's (2009) advice included bringing wild animals into captivity at the rate of one migrant per 1–2 generations and fragmenting the captive population if the founding population is large. These are interesting parameters that would be important inclusions in future models. Overall, these simulations reinforce the importance of existing ideas, such as that relaxed selection increases trait variance and population persistence decreases with population size. It also emphasizes the fact that long-term monitoring is essential to effective reintroduction planning.

Our results also highlight some ideas that are not generally considerations in reintroduction planning and in our opinions should be – namely that increased variance in captive-bred populations and subtle changes in the release habitat can have a profound effect on survivorship when captive-bred animals are reintroduced into the wild. In addition, we suggest that highly specialized species are much more difficult to re-establish in altered habitats, and that we must think about conservation on the ecosystem level in order to conserve individual species.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** [Relaxed selection increases trait variance and decreases reintroduction success in simulated populations].

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