Title: Improving species conservation plans under IUCN's One Plan Approach using quantitative genetic methods

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RH: Quantitative genetics and conservation breeding

Keywords: Adaptive potential, ex situ, ecological genetics, gene flow, genetic groups, phenotypic plasticity, translocation, zoos, One Plan Approach, WCC 2020 Resolution 079

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## Abstract

Human activities are resulting in altered environmental conditions that are impacting the demography and evolution of species globally. If we wish to prevent anthropogenic extinction and extirpation, we need to improve our ability to restore wild populations. *Ex situ* populations can be an important tool for species conservation. Quantitative genetic analysis can improve management of these populations and thus the success of *in situ* population management actions that they support. In this review we outline methods that could be used to improve the management of *in situ* and *ex situ* populations in a One Plan Approach. We discuss how quantitative genetic models can help measure genetic variation, phenotypic plasticity, and social effects on phenotypes. Finally, we discuss how phenotypic change can be predicted using measurements of additive genetic variance and selection. While previous work has highlighted the value of *ex situ* populations for the field of quantitative genetics, we argue that quantitative genetics can, in turn, offer opportunities to improve management and consequently conservation of populations of species at risk. We show that quantitative genetic analyses are a tool that could be incorporated into and improve *ex situ* management practices.

## Introduction

Widespread human landscape transformations are resulting in changing conditions for species across the globe (Parmesan 2006). Biodiversity is decreasing due to habitat loss, pollution, disease, and climate change and most countries have not achieved biodiversity targets for 2020 set to slow rates of species declines (United Nations Environment Program Convention on Biological Diversity, Aichi Target 12). This lack of progress calls for new approaches. In 2020, the IUCN World Conservation Congress passed a resolution promoting the integration of *in situ* (within a species' natural habitat) and *ex situ* (in human care outside a species' natural habitat) conservation interventions by applying the One Plan Approach (OPA; WCC-2020-Res-079n; Byers et al. 2013). Traditionally, species conservation planning has followed parallel but separate tracks: field biologists and wildlife managers' efforts to address conservation needs *in situ*, zoo, aquarium, and species-specific breeding centres (e.g. the United States Fish and Wildlife Service Black-footed Ferret Conservation Center), efforts to develop sustainable *ex situ* populations. Under the OPA developed by the IUCN's Conservation Planning Specialist Group (CPSG), species conservation planning is conducted in an integrated manner by all responsible parties, whether inside or outside of the natural habitat (Byers et al. 2013).

As recognized by the World Conservation Congress's 2020 Resolution 079, zoos and aquariums can be an essential component of efforts to reduce the rate of species loss and to improve the status of at risk species (Che-Castaldo, Grow, & Faust 2018;). However, *in situ* recovery efforts that rely on source animals from *ex situ* conservation breeding programs can face difficulties (Fischer & Lindenmayer 2000; Godefroid et al. 2011; Soorae 2021). The reproductive fitness of individuals released to the wild can be reduced because of genetic drift, inbreeding, and adaptation that might occur in captivity (Frankham 2008). Adaptation to captive conditions could result in phenotypes that are maladaptive in the wild, resulting in lower survival upon release, and adversely affect reintroduction efforts (Baskett, Burgess, & Waples 2013). Additionally, gene flow via introduced individuals may alter evolutionary processes in the wild resulting in negative effects on wild populations. We argue that some of these challenges can be addressed– through the incorporation of quantitative genetic management techniques– to improve *ex situ* population management, similar to that used to disentangle causes of phenotypic change in wild populations (Pelletier et al. 2009; Chargé et al. 2014). Monitoring phenotypic and genetic characteristics of *ex situ* populations would help to ensure their suitability for conservation efforts, in particular under the OPA, in which captive and wild populations are managed as a type of metapopulation (Byers et al. 2013).

Tracking the phenotypic dynamics of captive populations, and quantifying underlying processes leading to change could be an effective management tool to ensure *ex situ* populations will have a positive conservation impact (Princée 2016, Chapter 16). Many breeding programs follow a mate pairing method based on matching mean kinship derived from pedigrees in an effort to minimize genetic drift, inbreeding, and selection pressure while maintaining genetic diversity (Montgomery et al. 1997; Ralls et al. 2000; Willoughby et al. 2014; Ballou et al. 2020).

However, the realities of captive management (e.g. the unequal reproductive success of mate pairs and small effective population sizes) mean that evolutionary change can still occur (Schulte-Hostedde & Mastromonaco 2015). Optimal breeding designs will not always be feasible given a breeding program's resources and outcomes of any given captive management plan could deviate from expectations because of unaccounted for influences. Deviation from an optimal design either because it is not feasible or because of unaccounted factors could lead to evolutionary change. For example, a study of Houbara Bustards (*Chlamydotis undulata*) revealed evolutionary change in gamete production, courtship display rate, and body mass caused by unintentional selection in captivity over just 5 generations (14 years) despite a breeding management strategy based on mean kinship (Chargé et al. 2014).

Conservation breeding programs could be improved in many cases through analysis of phenotypes. Herein, we undertake a review of quantitative genetics tools that we suggest can be incorporated into *ex situ* population management, thereby improving the success of OPA conservation efforts by quantifying, and ultimately preventing genetic adaptation to captivity (Williams & Hoffman 2009). We describe methods that have been used in the study of ecological and evolutionary dynamics in wild populations, expanding upon a previous review by (Pelletier et al. 2009), including updated information on available tools, and suggesting how they can be extended to *ex situ* populations (Fig. 1). First, we review why it is valuable for breeding managers to monitor phenotypic dynamics (Section 1). Next, we describe how the plastic and evolutionary dynamics of traits in captivity can be measured and we discuss how these measurements can be used to improve the success of OPA conservation programs. We focus on three major areas of consideration, including the measurement of evolutionary change (Section 2), phenotypic plasticity (Section 3), and parental and social effects (Section 4). Finally, we describe the integration quantitative genetic information into current conservation breeding practices to help inform *ex situ* and *in situ* conservation management and conclude with tools that could be used to try to measure and predict adaptation (Section 5). We provide introductory papers to allow managers to begin to monitor these processes in their breeding programs (Fig. 2).

## 1. Phenotypic change in captivity

Phenotypic differences in behaviour and morphology can occur between wild and captive-bred individuals (O'Regan & Kitchener 2005; McDougall et al. 2006), which could  decrease fitness in the wild (Jolly & Phillips 2021). Differences between captive and wild phenotypes can be caused by phenotypic plasticity, changes in demographic structure, evolutionary change, or all processes. Phenotypic plasticity is the range of phenotypes an individual (or genotype) expresses across a range of environmental conditions, while evolutionary change is a change in allele frequencies underlying phenotypes caused by mutation, gene flow, genetic drift, and selection (West-Eberhard 2003; Walsh & Lynch 2018).

The captive environment can potentially alter a broad range of traits. Morphological changes have been commonly observed to change due to the captive environment (Courtney Jones, Munn, & Byrne 2018; Fischer & Romero 2019). For example, differences in nutritional environment and a change in physical activity can alter tissue development (Harbers et al. 2020). Cues or social interactions that prompt development may also be altered in captivity (Monaghan 2008; Sultan 2015). Additionally, capture biases and the captive environment can inadvertently select for specific behavioural temperaments resulting in differences between the temperament of wild and captive individuals (McDougall et al. 2006; Monk et al. 2021).

Measurements of plastic trait responses and the genetic variation present in traits can both provide information on the adaptive potential of the population and alert managers to potentially unwanted evolutionary change (Section 2; Section 5). Even if captive and wild individuals exhibit the same average phenotype, phenotypic plasticity could be masking evolutionary change (*e.g.* Bonnet et al. 2017). For example, smaller individuals might be selected for in a captive environment but better nutrition could result in increases in size that would mask this evolutionary change. Only after being released into the wild where food resources are limited or more difficult to acquire, would the evolutionary change towards a smaller size become apparent.

Monitoring and quantifying evolutionary processes is of interest to *ex situ* population managers because phenotypic change induced by captivity has been observed to reduce survival and reproduction in the wild (Sundström et al. 2016; Cox and Lima 2006; Blumstein et al. 2002; Griffin et al. 2001). Further, change in captivity could alter the ecological role of the organism or the societal value of organism. As the goal of *ex situ* populations is the restoration of viable self-sustaining populations, we argue it is useful to understand environmental and genetic contributions to phenotypes in captivity. Quantitative genetics provides a toolset for disentangling the processes of evolutionary change and phenotypic plasticity. Quantitative genetics is routinely used in breeding programs for domestic livestock (Walsh & Lynch 2018). This methodology has also led to insight into the evolutionary dynamics in wild populations (Charmantier, Garant, & Kruuk 2014) and it has been highlighted that zoo populations may provide datasets, in the form of studbooks, well suited to quantitative genetic analysis (Pelletier et al. 2009). Further, while molecular methods can help to track or identify loss of diversity in genetic markers, changes in neutral genetic diversity do not always correspond well to changes in adaptive genetic variation (Reed & Frankham 2001; Mittell, Nakagawa, & Hadfield 2015; Lacy, Malo, & Alaks 2018). Thus, ideally, *ex situ* populations are managed through monitoring of overall molecular genetic variation, quantitative genetic variation (the phenotypic variation ascribed to molecular genetic variation), and the non-genetic causes of phenotypic variation.

## 2. Evolutionary change

### 2.1 Trends in breeding values

Quantitative genetic approaches use statistical tools to separate measured phenotypes into genetic and environmental components, allowing the statistical quantification of potential evolutionary change. Using a quantitative genetics approach, those managing *ex situ* populations need information on pairwise additive relatedness (acquired through a pedigree, partial kinship information, or molecular markers) and phenotypic data, combined in statistical models to evaluate whether evolutionary change might be occurring in their captive population (Fig. 1). Historically, quantitative genetic analysis was focused on laboratory and agricultural studies where experimental breeding crosses were possible, but statistical techniques developed in the 1950s (Henderson 1950) and computational advances in the late 1990s allowed widespread use of the "Animal Model." The Animal Model is a form of mixed model that uses relatedness among individuals to estimate the additive genetic variation of a trait (Wilson et al. 2010); it models an individual's phenotype as a function of the population mean phenotype plus an additive genetic value and residual error. The additive genetic value, or the breeding value, represents the additive genetic difference of an individual and the population average, or the sum of the average effects of all the alleles the individual carries (Falconer & Mackay 1996; Lynch & Walsh 1998). Changes in the average breeding value of a trait over time in a population can be an indication of evolutionary change (Hadfield et al. 2010). Livestock producers are often interested in changing the average breeding value of a population so that it is better for production, for example in milk yield (Rendel & Robertson 1950), while evolutionary ecologists are interested in determining how and whether evolutionary change is occurring in a wild population (Walsh & Lynch 2018). In contrast, those maintaining *ex situ* populations for conservation purposes will probably be interested in maintaining the average breeding value of a trait in the captive population and the variance of the breeding values (the additive genetic variance) in the interest of avoiding evolutionary change and maintaining adaptive potential (Williams & Hoffman 2009). Minimizing mean kinship will reduce allele frequency change and depending on the kinship matrix used managers can maximize the amount genetic variation or maintain allele frequencies closer to the base population (Meuwissen et al. 2020; Morales-González; Saura et al. 2008). However, monitoring and controlling breeding values for specific traits could be combined with management plans to identify and control potential evolutionary change. There is often uncertainty associated with each estimate of a breeding value, and ignoring this error in the analysis of trends in breeding values can lead to an incorrect analysis (Hadfield et al. 2010; Houslay & Wilson 2017; Princée 2016, Chapter 16) however, there are techniques such as multivariate statistics or Bayesian analysis that can help with some of these issues (Fig. 2).

When working with a captive population that is maintained across multiple facilities, managers will also want to account for differences in phenotype between facilities and understand how much of any observed variance different management practices among facilities. Shared environmental effects such as year, rearing location, and parental effects should also be accounted for in any estimation of the additive genetic variance because these values can inflate similarity among relatives and bias estimates of the additive genetic variance. The same tools that estimate additive genetic variance can also be used to account for such groupings in the data. The use of mixed or hierarchical models in quantitative genetics is used to disentangle components of variance beyond just components of genetic variance (Fig. 2). Given the proper grouping (*e.g.* cohort year or rearing facility) is included in the data, we can estimate the contribution of such a grouping to the total phenotypic variance. In some cases, the variance associated with different people taking phenotypic measurements can be quantified and accounted for in the measurement of heritability or repeatability of a trait (Ponzi et al. 2018). Because of the relatively small size of captive populations, non-additive genetic variation and increased inbreeding could also contribute to variation in traits (Wade & Goodnight 1998). Quantitative genetics provides useful tools for measuring the impact of these genetic effects on observed phenotypes and may help quantify evolutionary changes in captivity more accurately (Pelletier et al. 2009; Wolak & Keller 2014). Our review is timely because recent genomic tools will make quantitative genetic analyses possible in a broader range of species and populations (Gienapp et al. 2017; e.g. Gervais et al. 2019). Genomic relatedness matrices can now be used in lieu of a pedigree derived relatedness and implemented in an Animal Model approach to estimate the additive genetic variances of traits in species where it previously was not possible. Further, genomic tools can help to clarifying relationships among founding individuals in a population and connect descendants of released individuals to lineages in the captive population.

Building an Animal Model to estimate evolutionary change using breeding values will require a significant up-front time investment, but analysis can provide invaluable information for management of quantitative genetic variation that cannot easily be estimated by other methods. Further, once a suitable model has been developed it can be updated annually to monitor any potential evolution occurring in traits of interest in the captive population over time. Managers could then try to alleviate known or likely drivers of evolutionary change (see section 5). If changes in the average breeding values are determined to be of concern, managers could increase gene flow from wild populations or to drive breeding values in a desired direction through selective breeding. Increasing gene flow and selective breeding comes with difficulties and depends on sampling individuals from the wild that have breeding values that can alter the average captive breeding value in a desired direction. Knowledge of the wild population will help inform strategies that use gene flow to alleviate evolutionary change in captivity (e.g. sampling relatives from families with estimated breeding values in captivity). Selective breeding should be done with caution because it could reduce genetic diversity and have unintended consequences through selection on correlated traits (Ralls et al. 2000; Lande & Arnold 1983; Arnold & Wade 1984a, 1984b).

Quantitative genetic analyses will be limited by the amount of data available for a managed population. In some cases, an additive genetic variance estimate will be possible with 100 or fewer animals, but statistical power in these analyses also depend on the number of relatives in a pedigree, the structure of the pedigree, and covariation of relatives with confounding variables (e.g. maternal effects, rearing facility). Given a specific studbook pedigree, a manager could conduct a simple power analysis to try to determine the heritability they would be able to estimate with their specific pedigree structure (Hadfield et al. 2010; Morrissey & Wilson 2010).

## 2.2 Genetic Groups

Founders in a population might come from populations with different genetic backgrounds that might have traits with different average breeding values. Using genetic groups, Animal Model methodology can account for known or assumed genetic structuring in a studied population (Wolak & Reid 2017; Lacy 2012). Genetic groups are researcher defined groupings that are ideally informed by knowledge of assumed or known genetic structuring in the wild (founders from distant populations or molecular marker informed population structuring). One valuable approach for joint *ex situ* and *in situ* management could be to assign founding individuals, and progeny produced in the first few years of a conservation breeding program to one group, and later immigrants brought into captivity as a second group. The proportion of each offspring's genome attributed to the *ex situ* versus *in situ* population can then be determined using the studbook pedigree. Beyond just accounting for biases, partitioning individuals among genetic groups in this way allows explicit measurement of the effects of wild population gene flow on an average trait value in the captive population (Wolak & Reid 2017). A difficult decision for managers will be to determine the number of genetic groups to use for a given conservation program. For example, after how much time should new individuals brought into captivity be considered a new genetic group? Analysis of molecular markers could possibly help inform the number of groups to use in a genetic group analysis. If enough data are available in the wild, trait values could also be monitored and quantified for the *in situ* population, which would provide comparisons to help determine the extent to which captive individuals differ from a baseline (Fig. 1). Additionally, recent advances in analytical methods allow for the measurement of different additive genetic variances between groupings and extend genetic group methods to genomic relatedness, which may be useful for comparing the adaptive potential of a trait in the wild or captive population (Muff et al. 2019; Aase et al. 2022). A study of song sparrows (*Melospiza melodia*) on Mandarte Island, Canada provides an empirical example of a genetic group model that mirrors an *ex situ* breeding program (i.e. a focal study population with measured and periodic gene flow). In this case, the analysis used a genetic group model to determine that gene flow to the island population is preventing local adaptation (Reid et al. 2020).

## 3. Plasticity and changes in plasticity

Phenotypic plasticity is the range of phenotypes that a single genotype, and in some cases individual, can express across a range of environmental conditions (Sultan 2015; West-Eberhard 2003). Individuals can differ in their plastic responses to the same environmental gradient (Box 1; Fig. 3). Like variation in a phenotype, the variation in an individual's plastic response to environmental conditions can be decomposed into environmental and genetic contributions (Gienapp & Brommer 2014). If individuals differ in their plastic responses because of genetic differences, plastic responses themselves could evolve. Therefore, captivity might influence plastic responses through evolutionary change or environmental/developmental effects that alter an individual's plastic response. Most importantly, an altered plastic response might affect the fitness of an individual or family in captivity or the wild, which is why managers must be concerned with the response.

To measure individual (combined environmental and additive genetic response; individual by environment reaction norms; IxE; Fig. 3 B, C) plastic responses to captivity, repeated measures on previously-captive individuals in wild environment are required (Nussey, Wilson, & Brommer 2007; Box 1). This approach highlights the benefits of and need for an OPA management strategy when *ex situ* populations are incorporated into species conservation. For non-clonal species, we can most easily measure the individual level plastic responses (IxE; Fig. 3 B, C) of labile traits that are expressed multiple times in an individual's life (annual fecundity, timing of breeding, migratory urge). The genotypic component (genotype by environment interaction; GxE; Fig. 3D, E) of a response to captivity might be more easily measured and relevant to managers. Measuring GxE interactions will require the measurement of phenotypes from groups of relatives in the wild and captivity. GxE interactions could inform managers how a group of related individuals might perform in the wild and captivity (Fig. 3E).

Understanding how captivity shapes plastic responses to environmental conditions individuals will encounter *in situ* may be one of the most important considerations in a reintroduction program. The captive environment differs in many ways from the wild environment, and both genetic and environmental differences between individuals may cause them to respond differently. Captivity could affect the plasticity of traits and the ability of individuals to plastically respond to environmental variation. Some traits might revert to wild values post-release, while others may not (Fig. 4). For example, plastic responses may be adaptive in natural environmental conditions, and plasticity is now increasingly recognized as a primary response to changing climatic conditions (Bonamour et al. 2019) . Early-life stages are particularly sensitive to environmental conditions (English et al. 2016; West-Eberhard 2003). Consequently, development during early-life in a captive environment could affect the way an individual responds to environmental variation once released (Munch et al. 2018), and thus its fitness. Finally, anti-predator behaviours will be valuable to monitor as they are sometimes, but not always, observed to disappear over time in captivity (Cox & Lima 2006; Blumstein et al. 2002) and anti-predator behavioural training may help improve survival upon release (Reading et al. 2013; Griffin et al. 2001; but see Moseby et al. 2012)

The consequences of changes to plasticity depend on whether the ability to plastically respond to environmental conditions affects fitness for a given species in the wild. For example, if there is a positive association between how quickly an individual responds to environmental variation (the slope of the plastic response) and fitness (Fig. 5A), reduced plastic responses caused by captivity could negatively impact the success of reintroduction or supplementation efforts. That said, if there is no relationship observed between fitness and the plastic response (Fig. 5D) it may not be as important to monitor or put effort into determining how to prevent the loss of this response during captive management. While likely challenging to measure, it may be worthwhile to investigate if and how (and how commonly) captivity alters plastic responses in wild conditions and how to create environmental conditions in captivity that can maintain appropriate plastic responses in the wild.

A sampling design challenge will be to measure plastic responses of 1) wild individuals to captivity, 2) wild individuals to natural environmental variation, and 3) previously captive individuals to natural environmental variation (Fig. 4). Often hundreds of individuals are required for statistical power and each of these individuals needs to be repeatedly measured across environmental contexts (Dingemanse & Dochtermann 2013). Power analysis could be used to design data collection protocols that will ensure results can help improve a management programs ability to detect plasticity or whether an existing data set is adequate to statistically detect plasticity (Allegue et al. 2017).

**Box 1 Measuring plasticity**

Quantifying plasticity allows us to try to measure the contribution of non-genetic responses to environmental change to overall population level phenotypic change. Individual responses can be measured as a straight line connecting an individual's average phenotype in the captive and wild environment (Fig. 3). When the environmental variable in such an analysis is mean-centred the intercept of such a line indicates the average trait value of an individual and the slope connecting the environment-specific trait values indicates the individual’s response to captivity (Fig. 3). Individual plastic responses are usually measured in multilevel/hierarchical/mixed models (Martin et al. 2011). Within the studied population, individuals could have the same response (Fig. 3B) or might vary in their response to captivity (Fig. 3C). Differences among individuals could be caused by genetic or permanent environmental differences (environmental effects that have a persistent effect on an individual's phenotype; see (Kruuk 2004; Wilson et al. 2010). Like individual responses, family groups might have similar (Fig. 3D) or different responses (Fig. 3E) to captivity (Gienapp & Brommer 2014).

## 4. Parental and indirect genetic effects

Both parental effects and social interactions (*i.e.* indirect genetic effects on an individual caused by the expression of genes in another individual, either a parent or conspecific) can have effects on the phenotype of an individual. Indirect effects can be heritable and could impact the adaptive potential of a trait (*e.g.* Moiron et al. 2020). Because captivity could alter both parental effects and social interactions, the impacts of indirect genetic effect could vary drastically between wild and captive populations. Monitoring wild and captive social networks can allow measurement of the variance in a trait explained by interactions among individuals (Thomson et al. 2018). Detecting differences among social networks of captive and wild populations is important because of 1) the direct impacts a change in network might have on fitness or fitness related traits; and 2) the potential effects of an altered network on the rate of evolutionary change in captive versus wild environments.

In many species parents provide cues or care for offspring that can be altered by changes in environmental conditions which are likely to result from captivity (Munch et al. 2018). Because of the potential long-term impacts of an altered developmental environment, especially for captive-reared animals, it may be particularly important to study how the captive developmental environment affects offspring phenotypes (English et al. 2016). For example, in common marmosets (*Callithrix jacchus*) early life exposure to higher fat diets increases the probability of post-weaning obesity, and the milk from captive marmosets tends to have higher fat content than wild marmosets (Power et al. 2008; Tardif et al. 2013). Further, mother marmosets in captivity varied in their milk composition, suggesting that genetic and/or environmental differences exist among mothers that have health consequences for their offspring (Power, Oftedal, & Tardif 2002).

Beyond parental effects, social interactions among individuals can affect the phenotypes expressed in a population (Fisher, Haines, et al. 2019; Fisher, Wilson, et al. 2019; Laskowski, Wolf, & Bierbach 2016). For example, mates and neighbours can affect an individual's breeding time (Fisher & McAdam 2019). The impact of this social interaction has been observed in common terns (*Sterna hirundo*), where the breeding time of females is affected by their mate, and in North American red squirrels (*Tamiasciurus hudsonicus*), where breeding time can be influenced by neighbouring squirrels (Moiron et al. 2020; Fisher, Wilson, et al. 2019). Further, impacts of indirect genetic effects likely depend on the number of conspecifics an individual interacts with (Fisher & McAdam 2019), which has the potential to be altered by captivity.

## 5. Putting it all together: combining quantitative genetic analyses with conservation management tools

Application of quantitative genetics to *ex situ* and *in situ* conservation programs will be limited by the quality and amount of data available. Here we provide additional guidance for managers interested in collecting the data required to conduct quantitative genetic analyses, including available software, and standardized data collection. It may be most worthwhile for managers to begin with a trait that has changed over generations in captivity or is known (or hypothesized) to hamper breeding or reintroduction success (Fig. 6).

Studbooks for conservation breeding are routinely maintained in a variety of platforms, from Excel and Access databases to dedicated software such as Poplink (Faust et al. 2019). Currently approximately 1400 conservation studbooks are maintained in the web-based portal ZIMS for Studbooks (Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org ). Platforms provide varying options for data storage, manipulation, and export.

Regardless of format, studbooks typically include basic data that is needed for quantitative genetic analysis, in the form of pedigrees and life history events. Studbook pedigrees can be simple pedigrees noting discrete parentage but also allow for the incorporation of parentage "assumptions" that can be used to assign animals to groups in cases where pedigree is unknown or to create cohorts for the study of gene flow. Additionally, the commonly used studbook applications include an option to incorporate User Defined Data Fields (UDFs). UDFs can be used to record phenotypic data or quantitative genetics output such as breeding value. UDFs are flexible and can be updated which will be invaluable for estimated breeding values that will change and need to be updated every time a new analysis is conducted. Studbooks are databases commonly exported into analytical softwares (e.g. PMx, Ballou et al. 2020) that are used to determine mate-pairings through a mean kinship list. PMx can also be used to compile life history events, generate demographic life tables, determine fecundity rates, estimate breeding seasonality, and other metrics of interest in the study of phenotypic change. As with studbook softwares, PMx allows for the importation of UDF fields that can be added to mean kinship lists, such as breeding value, which can then be considered in constructing pairing decisions.

Therefore, the estimates of gene flow, social management, and breeding strategies which incorporate quantitative genetics analyses can be modeled and considered alongside gene diversity (probability-based estimate of heterozygosity) retention and inbreeding coefficients to improve management.

The challenge remains, however, of how quantitative genetics can be incorporated into management paradigms for *ex situ* populations. Studbooks and associated analytical software including PMx and Vortex allow managers to explore how manipulating social groupings, housing conditions, husbandry methods, setting informed schedules of geneflow, and adjusting pair selection might impact current management (Lacy & Pollak. 2021).

Accurate studbook records and standardization of trait measurements are crucial for the preservation of a long-managed species; incorrect registration, administration errors, and limited founder information will compromise pedigree authenticity. Lineages and pedigree data must be accurate for effective application of quantitative genetic analyses; although some genetic variances can still be estimated without bias if errors in paternity assignment are random (Charmantier & Réale 2005; Firth et al. 2015). Pairing recommendations, either using quantitative genetics or traditional pedigree-based inbreeding coefficients, will always be presented with logistical and statistical limitations. Despite these limitations, the use of quantitative genetics in study systems with adequate data and with proper acknowledgement of uncertainty present the potential to improve management of *ex situ* and *in situ* recovery programs.

In our view, the key promise that quantitative genetics provides to conservation breeding programs is the ability to disentangle the processes that lead to phenotypic change in captivity. Quantifying the relative contribution processes to phenotypic changes will enable adaptive management and a prioritization of resources to the processes that most contribute to changes in captivity. Quantitative genetic techniques provide a set of tools that allow us to try to determine if more (or less) effort is needed to prevent causes of phenotypic change in captivity (plasticity, evolution, social environment), in addition to current best practices mate-pairing based on mean kinship. We emphasize that the OPA recommended by the IUCN is cohesive with quantitative genetic tools because the effectiveness of quantitative genetic tools will improve with increasing data gathered jointly from *in situ* and *ex situ* populations.

If restoring previous ecological conditions for a species at risk is impossible, conservation must necessarily focus on maintaining or improving the adaptive potential of populations (Chevin & Lande 2010). As the goal of *ex situ* populations is, ultimately, the conservation of the species in the wild, their management must ensure that supported populations can adapt to changing conditions in the wild. Predicting such adaptation will depend on understanding how selection operates and is changing in the wild, how much additive genetic variance is present for selected traits, and the suite of plastic responses available to a population (Sultan 2015; Gienapp & Brommer 2014).

Determining whether and how any evolutionary or plastic responses result in demographic changes remains a challenge for population biologists (Hendry 2016; Janeiro et al. 2017). However, some models have been developed that try to predict when plasticity or evolution might prevent the extinction of a population (Vedder, Bouwhuis, & Sheldon 2013; Chevin & Lande 2010). A particularly important parameter is the additive genetic variance of fitness. The additive genetic variance of fitness should be equivalent, in theory, to the rate of adaptive genetic evolution  (Bonnet, Morrissey, & Kruuk 2019; Fisher 1930; de Villemereuil et al. 2016). Thus, comparison of the additive genetic variance of fitness might indicate how quickly adaptive genetic evolution is occurring in wild versus captive populations. The goal of *ex situ* populations is ultimately to directly support conservation efforts for wild populations, for example through population augmentation. As such, *ex situ* and *in situ* partners should work together to quantify the wild population as changes due to captivity will directly impact program success, which is the intent of the OPA.

## Conclusions

Integrated planning and management of wild and captive populations in an OPA can improve the impact of conservation efforts for species at risk (Lees et al. 2021). Here, we present and provide support for the argument that quantitative genetic analysis is a powerful tool that can be used to enhance *ex situ* population management, and help to integrate *ex situ* and *in situ* activities. Several examples exist demonstrating how phenotypes have come to differ between captive and wild populations, despite best management practices for *ex situ* populations that include efforts to reduce the loss of diversity. The consequences of these differences are not always known, but, may impact the fitness of individuals that are used to directly support *in situ* conservation efforts. Using existing pedigrees and phenotypic data in the Animal Model approach, managers can disentangle the causes of these differences and understand their consequences. By extending the approach to include genetic groups, analyses can both quantify the effects of gene flow on phenotypes. Finally, these models can help managers to measure rates of adaptation in captivity or predict whether captive populations are maintaining the adaptive potential necessary to persist under changing conditions in the wild. Since the data to run quantitative genetics analyses often already exists (i.e. in studbooks), we see quantitative genetic analysis as a promising tool for conservation breeding that can likely be integrated with existing management methods used for maintaining genetic diversity. In doing so, *ex situ* populations will ensure they are as effective as possible in supporting *in situ* conservation efforts and managers can better identify where to direct limited resources to answer questions critical to improving the management of a species.

## Acknowledgements

We thank Alisa Samuelson for helpful comments. We respectfully acknowledge that Wildlife Preservation Canada's head office and African Lion Safari are situated on the homelands of the Anishinaabe, Haudenosaunee, and Attawandaron peoples, and on the treaty lands of the Mississaugas of the Credit First Nation. Further, we acknowledge that Queen’s University is situated on Anishinaabe and Haudenosaunee territory. We are grateful to be able to live and learn on these lands.

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## Figure Captions

**Figure 1:** Key questions that may arise in a conservation breeding program and the data and models that can be used in a quantitative genetic and One Plan Approach framework to answer

them. For each question references are provided that either provide code to run similar analyses or provide guides for the suggested model.

**Figure 2:** Introductory papers and resources for conservation managers looking to make use of quantitative genetic analyses for breeding programs.

**Figure 3:** Variation in plastic responses to captivity. If there is a plastic response at the population level (A) individuals  might all have the same plastic response (B) or they could differ in their responses to captivity (C). If individuals differ in their responses, these differences could be caused completely by environmental differences and we would not see differences among family groups (D) or  genetic differences might also have differences among families contributing to observed differences among individuals (E). We illustrate differences in responses as if they were completely caused by environmental (D) or genetic differences (E), but they can be caused by a combination of both environmental and genetic differences.

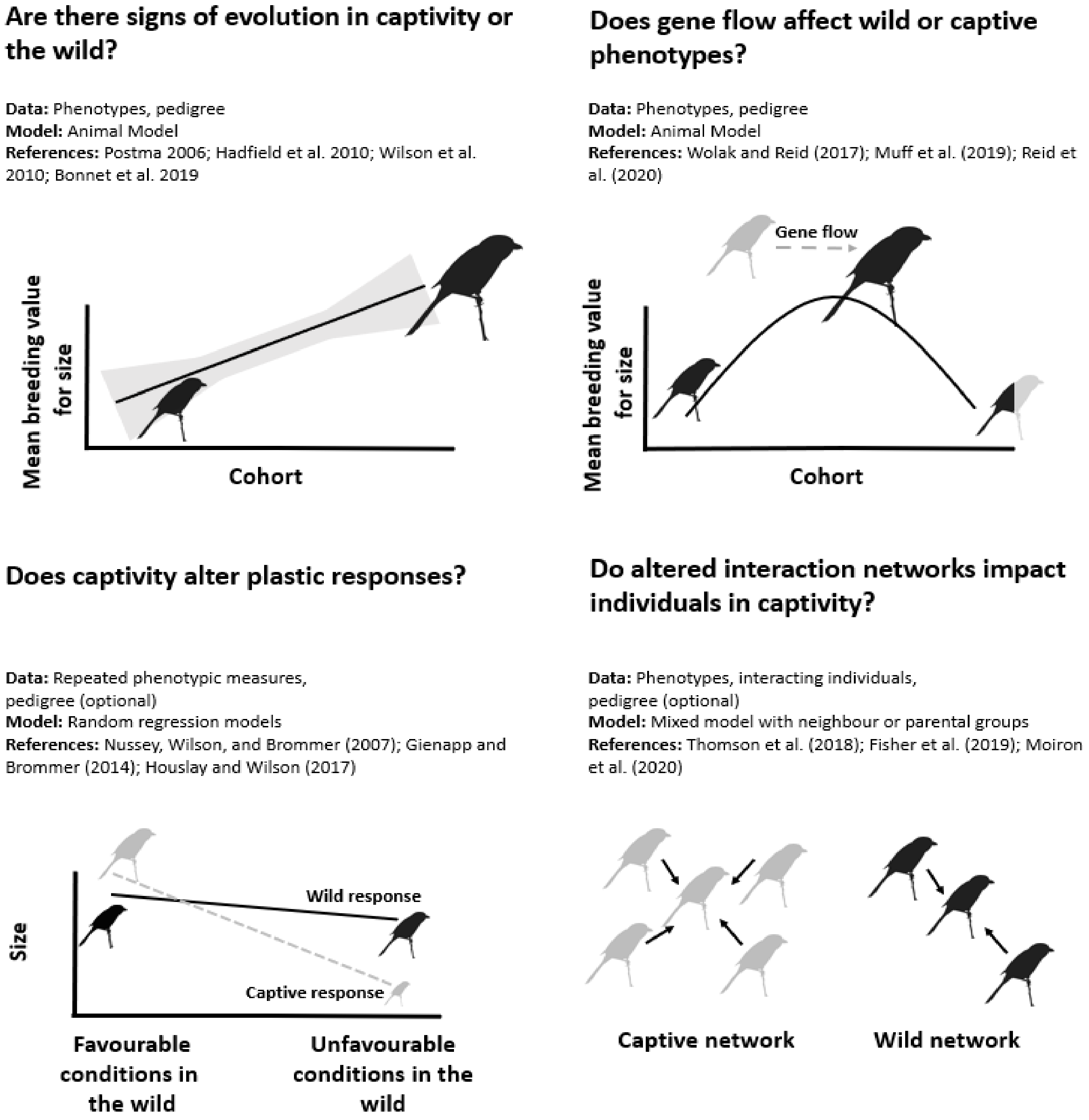
**Figure 4:** Three individual (or average family) responses to captivity. Responses to captivity between individuals might differ because of genetic or environmental effects. Individuals might not change a trait value to captivity at all (blue solid line), they may respond to captivity but then return to wild trait values when released (purple dashed line), or individuals might maintain the same captive phenotype despite returning to the wild environment (red dotted line).

**Figure 5:** Potential effects of captivity on the plastic response of a trait in the wild. Because of evolutionary or environmental effects in captivity the plastic response to environmental conditions post-release might be reduced or eliminated (A), or plastic responses post-release might remain similar to those in the wild (B). The consequences of changes in plasticity will depend on the relationship between plasticity and fitness in the wild. If plasticity is adaptive it

might play an important role for population persistence (C) or plasticity might not be important under wild environmental conditions (D).

**Figure 6:** A decision tree for determining the steps in an analysis aimed at disentangling the various causes in captivity that could contribute to changes in a trait.

## Figures



Are there signs of evolution in captivity or the wild?

**Data:** Phenotypes, pedigree
**Model:** Animal Model
**References:** Postma 2006; Hadfield et al. 2010; Wilson et al. 2010; Bonnet et al. 2019

Does gene flow affect wild or captive phenotypes?

**Data:** Phenotypes, pedigree
**Model:** Animal Model
**References:** Wolak and Reid (2017); Muff et al. (2019); Reid et al. (2020)

Does captivity alter plastic responses?

**Data:** Repeated phenotypic measures, pedigree (optional)
**Model:** Random regression models
**References:** Nussey, Wilson, and Brommer (2007); Gienapp and Brommer (2014); Houslay and Wilson (2017)

Do altered interaction networks impact individuals in captivity?

**Data:** Phenotypes, interacting individuals, pedigree (optional)
**Model:** Mixed model with neighbour or parental groups
**References:** Thomson et al. (2018); Fisher et al. (2019); Moiron et al. (2020)

**Fig. 1**

**Getting started with Animal Models**

Many of the papers on how to use an Animal Model have been written for ecologists studying populations in the wild. (i.e. *in situ* populations). Many of the concepts and tools will be similar for an analysis of a conservation breeding (*ex situ*) population.

- Wilson et al. (2010) is a good starting point reference that includes software that can be used for quantitative genetic analyses
- Pelletier et al. (2009) provide a perspective on using zoo populations to answer questions in quantitative genetics.
- Kruuk (2004) provides an in-depth overview of Animal Models

**Books**

- Charmantier, Garant, & Kruuk (2014) provide an overview of quantitative genetic techniques for wild populations.
- Falconer & Mackay (1996) provide an in-depth overview of the theory and analysis.
- Lynch & Walsh (1998) and Walsh & Lynch (2018) write detailed backgrounds on many quantitative and population genetic topics and are helpful references for more details on many concepts.
- Chapter 16 of Princée (2016) is an overview of quantitative genetic concepts and helpful guide for using studbooks to do quantitative genetic work.

**Breeding Values**

- Postma (2006) and Hadfield (2010) discuss statistical concerns in the analysis of breeding values
- Work on big horned sheep (Pigeon et al. 2016), snow voles (Bonnet et al. 2017), and red deer (Bonnet et al. 2019) include example R code for examining trends in breeding values

**Measuring Plasticiy**

There is broad literature on measuring plastic responses in the context of behaviour, climate change, and experimental studies that will be useful to managers trying to use existing data to measure plastic responses to captivity (Gienapp & Brommer 2014).

- Houslay & Wilson (2017) provide useful tutorials for quantifying individual level plasticity and measuring selection on plasticity using the R package MCMCglmm.
- From a perspective of behavioural traits detailed guidelines on the sampling schemes needed to measure different components of plasticity are provided by Dingemanse & Doctermann (2013) and Allegue et al. (2017) provide education software and a guide to the statistical quantification of individual differences.

**Genetic Groups, Inbreeding, and Dominance Genetic Variance**

- Wolak & Reid (2017) provide an explanation of genetic groups and code for running a basic analysis and Muff et al. (2019) extends their analysis to allow for different additive genetic variances among groups.
- Tools, software, and tutorials for examining inbreeding effects and estimating dominance genetic variance are provided by Wolak & Keller (2014) and Wolak (2012).

**Measuring Selection and Adaptive Potential**

Using associations between fitness and our trait of interest we can try to determine if our studied trait is under selection captivity.

- Lande and Arnold (1983) provide the classic and widely used multiple regression method for measuring selection
- Estimates of selection combined with information on heritability of traits can be used to predict responses to selection and compared to the observed trends to evaluate a hypothesis of selection in captivity causing evolutionary change (Queller 2017; Price 1970; Walsh & Lynch 2018)
- Bonnet et al. (2019) measure selection to compare observed and predicted evolutionary changes

**Social networks**

Differences in social networks over time and between wild and captive environments might contribute to phenotypic changes observed.

- Thomson et al. (2018) provide a tutorial on using Animal Models with multiple matrices to estimate non-genetic contributions to phenotypic variance (including social interactions)

**Fig. 2**

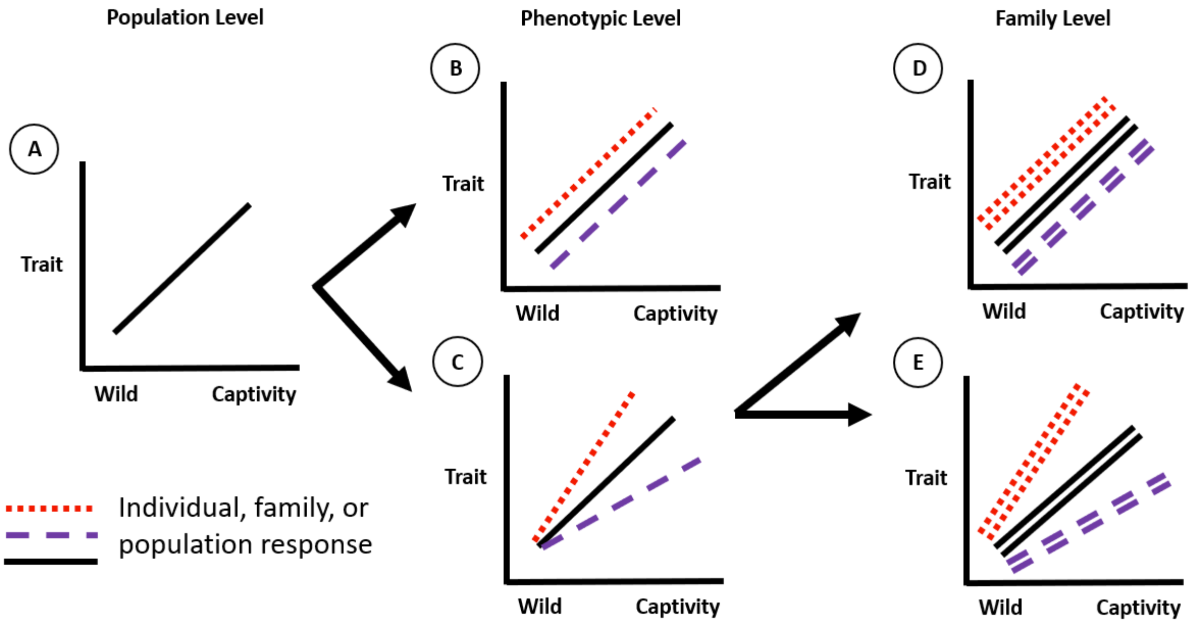

Population Level
Phenotypic Level
Family Level
A
B
C
D
E
Trait
Wild
Captivity
Individual, family, or population response

Fig. 3

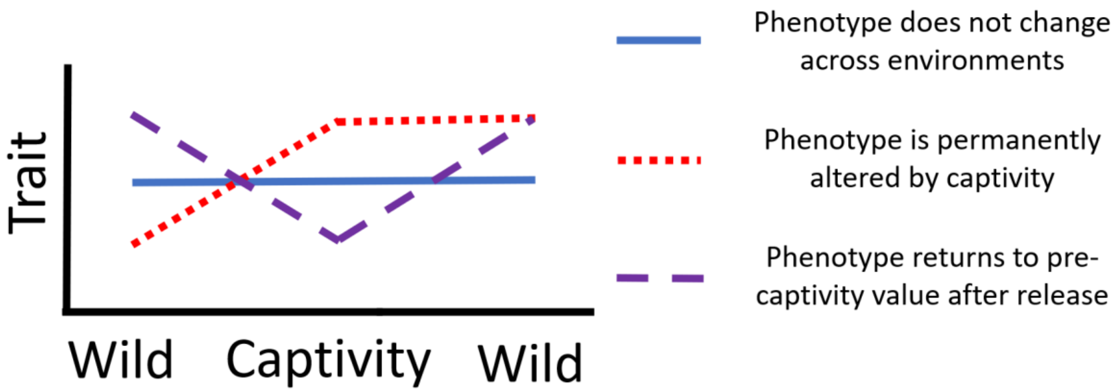

Trait
Wild
Captivity
Wild
Phenotype does not change across environments
Phenotype is permanently altered by captivity
Phenotype returns to pre-captivity value after release

**Fig. 4**

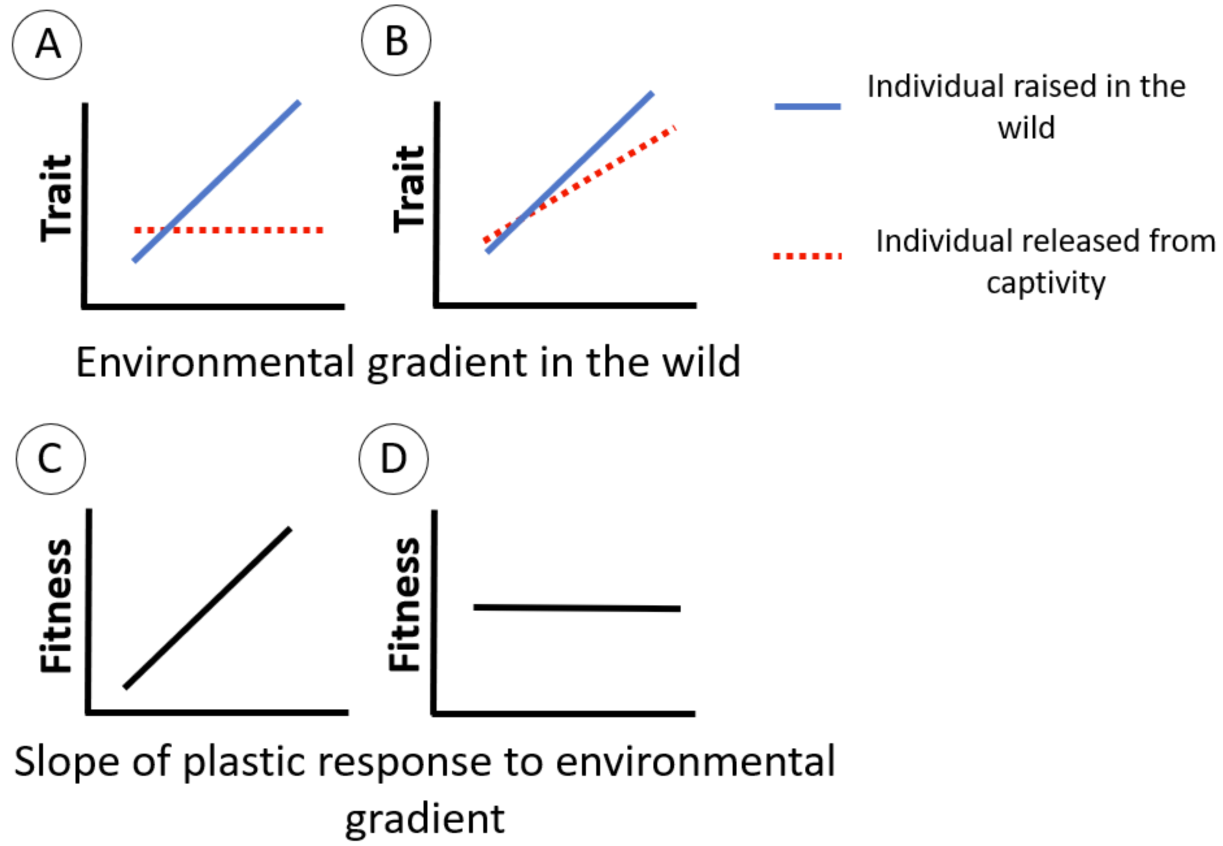

A
B
Trait
Trait
Individual raised in the wild
Individual released from captivity
Environmental gradient in the wild
C
D
Fitness
Fitness
Slope of plastic response to environmental gradient

**Fig. 5**

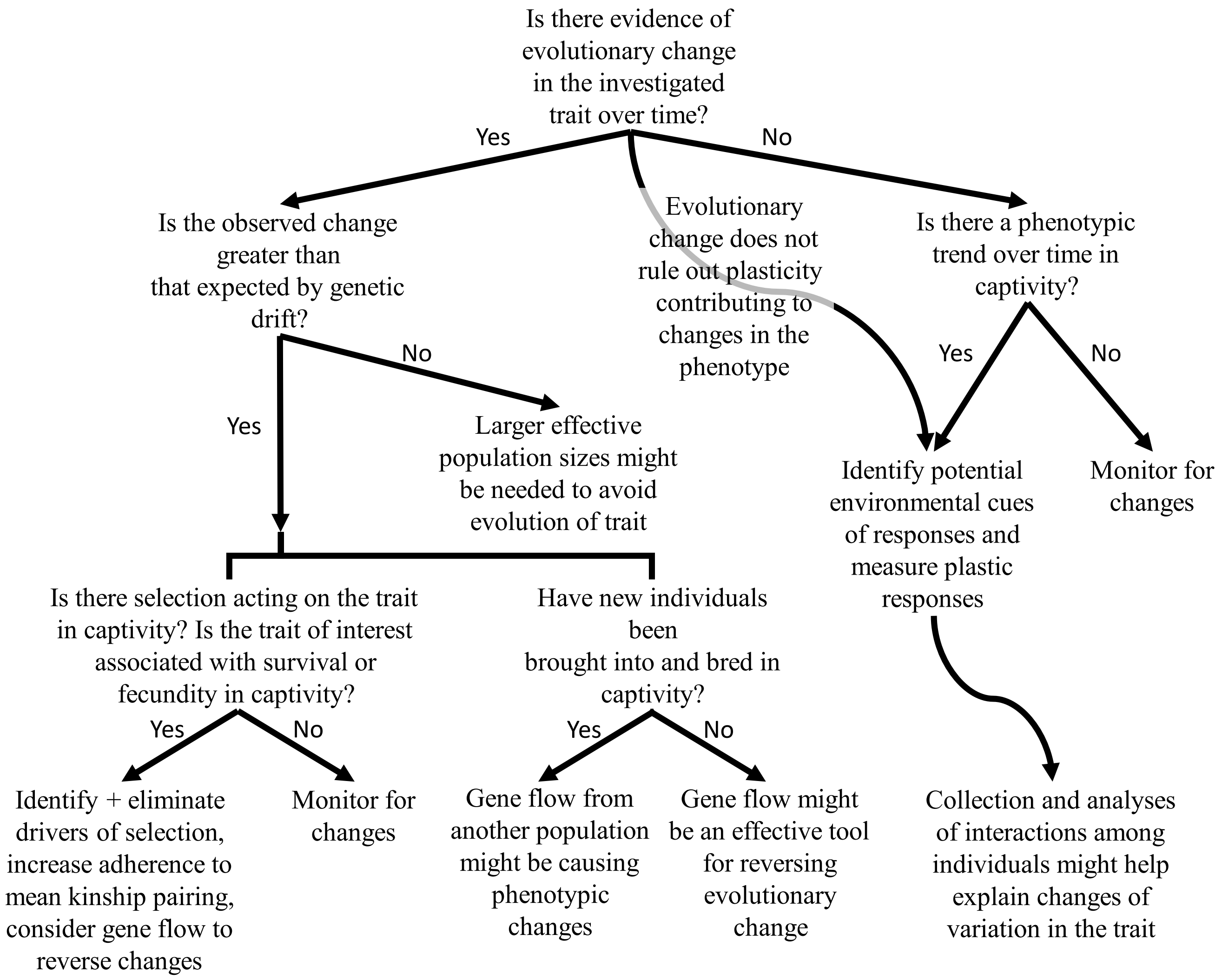

Is there evidence of evolutionary change in the investigated trait over time?
Yes
No
Is the observed change greater than that expected by genetic drift?
Evolutionary change does not rule out plasticity contributing to changes in the phenotype
Is there a phenotypic trend over time in captivity?
No
Yes
Larger effective population sizes might be needed to avoid evolution of trait
Yes
No
Identify potential environmental cues of responses and measure plastic responses
Monitor for changes
Is there selection acting on the trait in captivity? Is the trait of interest associated with survival or fecundity in captivity?
Have new individuals been brought into and bred in captivity?
Yes
No
Yes
No
Identify + eliminate drivers of selection, increase adherence to mean kinship pairing, consider gene flow to reverse changes
Monitor for changes
Gene flow from another population might be causing phenotypic changes
Gene flow might be an effective tool for reversing evolutionary change
Collection and analyses of interactions among individuals might help explain changes of variation in the trait

**Fig. 6**