

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

3 Drew Sauve¹, Jane Hudecki², Jessica Steiner², Hazel Wheeler², Colleen Lynch³, Amy A.
4 Chabot^{1,4}

5 ¹Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

6 ²Wildlife Preservation Canada, 5420 Highway 6 North, Guelph, Ontario N1H 6J2

7 ³Riverbanks Zoo and Garden, 500 Wildlife Parkway, Columbia, South Carolina USA 29210

8 ⁴African Lion Safari, 1386 Cooper Road, Cambridge, Ontario N1R 5S2

9 RH: Quantitative genetics and conservation breeding

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

12 Corresponding Author: Drew Sauve, 0as69@queensu.ca, Department of Biology, Queen's
13 University, Kingston, Ontario K7L 3N6, Canada

14 **Abstract**

15 Human activities are resulting in altered environmental conditions that are impacting the
16 demography and evolution of species globally. If we wish to prevent anthropogenic extinction
17 and extirpation, we need to improve our ability to restore wild populations. *Ex situ* populations
18 can be an important tool for species conservation. However, it is difficult to prevent deviations
19 from an optimal breeding design and altered environments in captivity seem likely to lead to
20 evolutionary or plasticity-induced phenotypic change that could make reintroduction more
21 difficult. Quantitative genetic analysis can help disentangle the causes of phenotypic change in
22 *ex situ* populations. Consequently, quantitative genetics can improve the management of these

23 populations and the success of *in situ* population management actions that they support. In this
24 review we outline methods that could be used to improve the management of *in situ* and *ex situ*
25 populations in a One Plan Approach. We discuss how quantitative genetic models can help
26 measure genetic variation, phenotypic plasticity, and social effects on phenotypes. Finally, we
27 discuss how phenotypic change can be predicted using measurements of additive genetic
28 variance and selection. While previous work has highlighted the value of *ex situ* populations for
29 the field of quantitative genetics, we argue that quantitative genetics can, in turn, offer
30 opportunities to improve management and consequently conservation of populations of species
31 at risk. We show that quantitative genetic analyses are a tool that could be incorporated into and
32 improve *ex situ* management practices.

33 **Introduction**

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

46 populations. Under the OPA developed by the IUCN's Conservation Planning Specialist Group
47 (CPSG), species conservation planning is conducted in an integrated manner by all responsible
48 parties, whether inside or outside the natural habitat (Byers et al. 2013).

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

66 Tracking the phenotypic dynamics of captive populations, and quantifying underlying
67 processes leading to change could be an effective management tool to ensure *ex situ* populations
68 will have a positive conservation impact (Princée 2016, Chapter 16). Many breeding programs

69 follow a mate pairing method based on mean kinship and inbreeding avoidance derived from
70 pedigrees to minimize genetic drift, inbreeding, and selection pressure while maintaining genetic
71 diversity (Montgomery et al. 1997; Ralls et al. 2000; Willoughby et al. 2014; Ballou et al. 2020).
72 However, the realities of captive management (*e.g.* the unequal reproductive success of mate
73 pairs and small effective population sizes) mean that evolutionary change can still occur
74 (Schulte-Hostedde & Mastromonaco 2015). Optimal breeding designs will not always be feasible
75 given a breeding program's resources and outcomes of any given captive management plan could
76 deviate from expectations because of unaccounted for influences. Deviation from an optimal
77 design either because it is not feasible or because of unaccounted factors could lead to
78 evolutionary change. For example, a study of Houbara Bustards (*Chlamydotis undulata*) revealed
79 evolutionary change in gamete production, courtship display rate, and body mass caused by
80 unintentional selection in captivity over just 5 generations (14 years) despite a breeding
81 management strategy based on mean kinship (Chargé et al. 2014).

82 Conservation breeding programs could be improved in many cases through analysis of
83 phenotypes. Herein, we undertake a review of quantitative genetics tools that we suggest can be
84 incorporated into *ex situ* population management, thereby improving the success of OPA
85 conservation efforts by quantifying, and ultimately preventing genetic adaptation to captivity
86 (Williams & Hoffman 2009). We describe methods that have been used in the study of
87 ecological and evolutionary dynamics in wild populations, expanding upon a previous review by
88 (Pelletier et al. 2009), including updated information on available tools, and suggesting how they
89 can be extended to *ex situ* populations (Fig. 1). First, we review why it is valuable for breeding
90 managers to monitor phenotypic dynamics (Section 1). Next, we describe how the plastic and
91 evolutionary dynamics of traits in captivity can be measured and we discuss how these

92 measurements can be used to improve the success of OPA conservation programs. We focus on
93 three major areas of consideration, including the measurement of evolutionary change (Section
94 2), phenotypic plasticity (Section 3), and parental and social effects (Section 4). Finally, we
95 describe the integration of quantitative genetic information into current conservation breeding
96 practices to help inform *ex situ* and *in situ* conservation management and conclude with tools
97 that could be used to try to measure and predict adaptation (Section 5). We provide introductory
98 papers to allow managers to monitor these processes in their breeding programs (Fig. 2).

99 **1. Phenotypic change in captivity**

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

108 The captive environment can potentially alter a broad range of traits. Morphological
109 changes have been commonly observed to change due to the captive environment (Courtney
110 Jones, Munn, & Byrne 2018; Fischer & Romero 2019). For example, differences in nutritional
111 environment and a change in physical activity can alter tissue development (Harbers et al. 2020).
112 Cues or social interactions that prompt development may also be altered in captivity (Monaghan
113 2008; Sultan 2015). Additionally, capture biases and the captive environment can inadvertently

114 select for specific behavioural temperaments resulting in differences between the temperament of
115 wild and captive individuals (McDougall et al. 2006; Monk et al. 2021).

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

124 Monitoring and quantifying evolutionary processes is of interest to *ex situ* population
125 managers because phenotypic change induced by captivity has been observed to reduce survival
126 and reproduction in the wild (Sundström et al. 2016; Cox and Lima 2006; Blumstein et al.
127 2002; Griffin et al. 2001). Further, change in captivity could alter the ecological role of the
128 organism or the societal value of organism. As one of the goals of *ex situ* populations is the
129 restoration of viable self-sustaining populations, we argue it is useful to understand
130 environmental and genetic contributions to phenotypes in captivity. Quantitative genetics
131 provides a toolset for disentangling the processes of evolutionary change and phenotypic
132 plasticity. Quantitative genetics is routinely used in breeding programs for domestic livestock
133 (Walsh & Lynch 2018). This methodology has also led to insight into the evolutionary dynamics
134 in wild populations (Charmantier, Garant, & Kruuk 2014) and it has been highlighted that zoo
135 populations may provide datasets, in the form of studbooks, well suited to quantitative genetic
136 analysis (Pelletier et al. 2009). Further, while molecular methods can help to track or identify

137 loss of diversity in genetic markers, changes in neutral genetic diversity do not always
138 correspond well to changes in adaptive genetic variation (Reed & Frankham 2001; Mittell,
139 Nakagawa, & Hadfield 2015; Lacy, Malo, & Alaks 2018). Thus, ideally, *ex situ* populations are
140 managed through monitoring of overall molecular genetic variation, quantitative genetic
141 variation (the phenotypic variation ascribed to molecular genetic variation), and the non-genetic
142 causes of phenotypic variation.

143 **2. Evolutionary change**

144 **2.1 Trends in breeding values**

145 Quantitative genetic approaches use statistical tools to separate measured phenotypes into
146 genetic and environmental components, allowing the statistical quantification of potential
147 evolutionary change. Using a quantitative genetics approach, those managing *ex situ* populations
148 need information on pairwise additive relatedness (acquired through a pedigree, partial kinship
149 information, or molecular markers) and phenotypic data, combined in statistical models to
150 evaluate whether evolutionary change might be occurring in their captive population (Fig. 1).
151 Historically, quantitative genetic analysis was focused on laboratory and agricultural studies
152 where experimental breeding crosses were possible, but statistical techniques developed in the
153 1950s (Henderson 1950) and computational advances in the late 1990s allowed widespread use
154 of the "Animal Model." The Animal Model is a mixed model that uses relatedness among
155 individuals to estimate the additive genetic variation of a trait (Wilson et al. 2010); it models an
156 individual's phenotype as a function of the population mean phenotype plus an additive genetic
157 value and residual error. The additive genetic value, or the breeding value, represents the
158 additive genetic difference of an individual and the population average, or the sum of the average
159 effects of all the alleles the individual carries (Falconer & Mackay 1996; Lynch & Walsh 1998).

160 Changes in the average breeding value of a trait over time in a population can indicate
161 evolutionary change (Hadfield et al. 2010). Livestock producers are often interested in changing
162 the average breeding value of a population so that it is better for production, for example in milk
163 yield (Rendel & Robertson 1950), while evolutionary ecologists are interested in determining
164 how and whether evolutionary change is occurring in a wild population (Walsh & Lynch 2018).
165 In contrast, those maintaining *ex situ* populations for conservation purposes will probably be
166 interested in maintaining the average breeding value of a trait in the captive population and the
167 variance of the breeding values (the additive genetic variance) in the interest of avoiding
168 evolutionary change and maintaining adaptive potential (Williams & Hoffman 2009).
169 Minimizing mean kinship will reduce allele frequency change and depending on the kinship
170 matrix used managers can maximize the amount genetic variation or maintain allele frequencies
171 closer to the base population (Meuwissen et al. 2020; Morales-González; Saura et al. 2008).
172 However, monitoring and controlling breeding values for specific traits could be combined with
173 management plans to identify and control potential evolutionary change. However, there is often
174 uncertainty associated with each estimate of a breeding value, and ignoring this error in the
175 analysis of trends in breeding values can lead to an incorrect analysis (Hadfield et al. 2010;
176 Houslay & Wilson 2017; Princée 2016, Chapter 16) however, there are techniques such as
177 multivariate statistics or Bayesian analysis that can help with some of these issues (Fig. 2).

178 When working with a captive population that is maintained across multiple facilities,
179 managers will also want to account for differences in phenotype between facilities and
180 understand how much of any observed variance is due to different management practices among
181 facilities. Shared environmental effects such as year, rearing location, and parental effects should
182 also be accounted for in any estimation of the additive genetic variance because these values can

183 inflate similarity among relatives and bias estimates of the additive genetic variance. The same
184 tools that estimate additive genetic variance can also be used to account for such groupings in the
185 data. The use of mixed or hierarchical models in quantitative genetics is used to disentangle
186 components of variance beyond just components of genetic variance (Fig. 2). Given the proper
187 grouping (*e.g.* cohort year or rearing facility) is included in the data, we can estimate the
188 contribution of such a grouping to the total phenotypic variance. In some cases, the variance
189 associated with different people taking phenotypic measurements can be quantified and
190 accounted for in the measurement of heritability or repeatability of a trait (Ponzi et al. 2018).
191 Because of the relatively small size of captive populations, non-additive genetic variation and
192 increased inbreeding could also contribute to variation in traits (Wade & Goodnight 1998).
193 Quantitative genetics provides useful tools for measuring the impact of these genetic effects on
194 observed phenotypes and may help quantify evolutionary changes in captivity more accurately
195 (Pelletier et al. 2009; Wolak & Keller 2014). Our review is timely because recent genomic tools
196 will make quantitative genetic analyses possible in a broader range of species and populations
197 (Gienapp et al. 2017; *e.g.* Gervais et al. 2019). Genomic relatedness matrices can now be used in
198 lieu of a pedigree derived relatedness and implemented in an Animal Model approach to estimate
199 the additive genetic variances of traits in species where it previously was not possible. Further,
200 genomic tools can help to clarifying relationships among founding individuals in a population
201 and connect descendants of released individuals to lineages in the captive population.

202 Building an Animal Model to estimate evolutionary change using breeding values will
203 require a significant up-front time investment, but analysis can provide invaluable information
204 for management of quantitative genetic variation that cannot easily be estimated by other
205 methods. Further, once a suitable model has been developed it can be updated annually to

206 monitor any potential evolution occurring in traits of interest in the captive population over time.
207 Managers could then try to alleviate known or likely drivers of evolutionary change (see section
208 5). If changes in the average breeding values are determined to be of concern, managers could
209 increase gene flow from wild populations or to drive breeding values in a desired direction
210 through selective breeding. Increasing gene flow and selective breeding comes with difficulties
211 and depends on sampling individuals from the wild that have breeding values that can alter the
212 average captive breeding value in a desired direction. Knowledge of the wild population will
213 help inform strategies that use gene flow to alleviate evolutionary change in captivity (*e.g.*
214 sampling relatives from families with estimated breeding values in captivity). Selective breeding
215 should be done with caution because it could reduce genetic diversity and have unintended
216 consequences through selection on correlated traits (Ralls et al. 2000; Lande & Arnold 1983;
217 Arnold & Wade 1984a, 1984b).

218 Quantitative genetic analyses will be limited by the amount of data available for a
219 managed population. In some cases, an additive genetic variance estimate will be possible with
220 100 or fewer animals, but statistical power in these analyses also depend on the number of
221 relatives in a pedigree, the structure of the pedigree, and covariation of relatives with
222 confounding variables (*e.g.* maternal effects, rearing facility). Given a specific studbook
223 pedigree, a manager could conduct a simple power analysis to try to determine the heritability
224 they would be able to estimate with their specific pedigree structure (Hadfield et al. 2010;
225 Morrissey & Wilson 2010).

226 **2.2 Genetic Groups**

227 Founders in a population might come from populations with different genetic backgrounds that
228 might have traits with different average breeding values. Using genetic groups, Animal Model

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

252 measured and periodic gene flow). In this case, the analysis used a genetic group model to
253 determine that gene flow to the island population is preventing local adaptation (Reid et al.
254 2020).

255 **3. Plasticity and changes in plasticity**

256 Phenotypic plasticity is the range of phenotypes that a single genotype, and in some cases
257 individual, can express across a range of environmental conditions (Sultan 2015; West-Eberhard
258 2003). Individuals can differ in their plastic responses to the same environmental gradient (Box
259 1; Fig. 3). Like variation in a phenotype, the variation in an individual's plastic response to
260 environmental conditions can be decomposed into environmental and genetic contributions
261 (Gienapp & Brommer 2014). If individuals differ in their plastic responses because of genetic
262 differences, plastic responses themselves could evolve. Therefore, captivity might influence
263 plastic responses through evolutionary change or environmental/developmental effects that alter
264 an individual's plastic response. Most importantly, an altered plastic response might affect the
265 fitness of an individual or family in captivity or the wild, which is why managers must be
266 concerned with the response.

267 To measure individual (combined environmental and additive genetic response;
268 individual by environment reaction norms; IxE; Fig. 3 B, C) plastic responses to captivity,
269 repeated measures on previously-captive individuals in wild environment are required (Nussey,
270 Wilson, & Brommer 2007; Box 1). This approach highlights the benefits of and need for an OPA
271 management strategy when *ex situ* populations are incorporated into species conservation. For
272 non-clonal species, we can most easily measure the individual level plastic responses (IxE; Fig. 3
273 B, C) of labile traits that are expressed multiple times in an individual's life (annual fecundity,
274 timing of breeding, migratory urge). The genotypic component (genotype by environment

275 interaction; GxE; Fig. 3D, E) of a response to captivity might be more easily measured and
276 relevant to managers. Measuring GxE interactions will require the measurement of phenotypes
277 from groups of relatives in the wild and captivity. GxE interactions could inform managers how
278 a group of related individuals might perform in the wild and captivity (Fig. 3E).

279 Understanding how captivity shapes plastic responses to environmental conditions
280 individuals will encounter *in situ* may be one of the most important considerations in a
281 reintroduction program. The captive environment differs in many ways from the wild
282 environment, and both genetic and environmental differences between individuals may cause
283 them to respond differently. Captivity could affect the plasticity of traits and the ability of
284 individuals to plastically respond to environmental variation. Some traits might revert to wild
285 values post-release, while others may not (Fig. 4). For example, plastic responses may be
286 adaptive in natural environmental conditions, and plasticity is now increasingly recognized as a
287 primary response to changing climatic conditions (Bonamour et al. 2019) . Early-life stages are
288 particularly sensitive to environmental conditions (English et al. 2016; West-Eberhard 2003).
289 Consequently, development during early-life in a captive environment could affect the way an
290 individual responds to environmental variation once released (Munch et al. 2018), and thus its
291 fitness. Finally, anti-predator behaviours will be valuable to monitor as they are sometimes, but
292 not always, observed to disappear over time in captivity (Cox & Lima 2006; Blumstein et al.
293 2002) and anti-predator behavioural training may help improve survival upon release (Reading et
294 al. 2013; Griffin et al. 2001; but see Moseby et al. 2012)

295 The consequences of changes to plasticity depend on whether the ability to plastically
296 respond to environmental conditions affects fitness for a given species in the wild. For example,
297 if there is a positive association between how quickly an individual responds to environmental

298 variation (the slope of the plastic response) and fitness (Fig. 5A), reduced plastic responses
299 caused by captivity could negatively impact the success of reintroduction or supplementation
300 efforts. That said, if there is no relationship observed between fitness and the plastic response
301 (Fig. 5D) it may not be as important to monitor or put effort into determining how to prevent the
302 loss of this response during captive management. While likely challenging to measure, it may be
303 worthwhile to investigate if and how (and how commonly) captivity alters plastic responses in
304 wild conditions and how to create environmental conditions in captivity that can maintain
305 appropriate plastic responses in the wild.

306 A sampling design challenge will be to measure plastic responses of 1) wild individuals
307 to captivity, 2) wild individuals to natural environmental variation, and 3) previously captive
308 individuals to natural environmental variation (Fig. 4). Often hundreds of individuals are
309 required for statistical power and each of these individuals needs to be repeatedly measured
310 across environmental contexts (Dingemanse & Dochtermann 2013). Power analysis could be
311 used to design data collection protocols that will ensure results can help improve a management
312 programs ability to detect plasticity or whether an existing data set is adequate to statistically
313 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).

314

315 **4. Parental and indirect genetic effects**

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

327 In many species parents provide cues or care for offspring that can be altered by changes
328 in environmental conditions which are likely to result from captivity (Munch et al. 2018).

329 Because of the potential long-term impacts of an altered developmental environment, especially
330 for captive-reared animals, it may be particularly important to study how the captive
331 developmental environment affects offspring phenotypes (English et al. 2016). For example, in
332 common marmosets (*Callithrix jacchus*) early life exposure to higher fat diets increases the
333 probability of post-weaning obesity, and the milk from captive marmosets tends to have higher
334 fat content than wild marmosets (Power et al. 2008; Tardif et al. 2013). Further, mother
335 marmosets in captivity varied in their milk composition, suggesting that genetic and/or
336 environmental differences exist among mothers that have health consequences for their offspring
337 (Power, Oftedal, & Tardif 2002).

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

347 **5. Putting it all together: combining quantitative genetic analyses with conservation** 348 **management tools**

349 Application of quantitative genetics to *ex situ* and *in situ* conservation programs will be limited
350 by the quality and amount of data available. Here we provide additional guidance for managers
351 interested in collecting the data required to conduct quantitative genetic analyses, including

352 available software, and standardized data collection. It may be most worthwhile for managers to
353 begin with a trait that has changed over generations in captivity or is known (or hypothesized) to
354 hamper breeding or reintroduction success (Fig. 6).

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

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

375 such as breeding value, which can then be considered in constructing pairing decisions.
376 Therefore, the estimates of gene flow, social management, and breeding strategies which
377 incorporate quantitative genetics analyses can be modeled and considered alongside gene
378 diversity (probability-based estimate of heterozygosity) retention and inbreeding coefficients to
379 improve management.

380 The challenge remains, however, of how quantitative genetics can be incorporated into
381 management paradigms for *ex situ* populations. Studbooks and associated analytical software
382 including PMx and Vortex allow managers to explore how manipulating social groupings,
383 housing conditions, husbandry methods, setting informed schedules of geneflow, and adjusting
384 pair selection might impact current management (Lacy & Pollak. 2021). Further, statistical
385 packages such as AlphaSimR can simulate different breeding designs allowing managers to
386 explore the impact a breeding decision might have on the genetics of a population (Gaynor et al.
387 2021).

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

397 uncertainty present the potential to improve management of *ex situ* and *in situ* recovery
398 programs.

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

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

416 Determining whether and how any evolutionary or plastic responses result in
417 demographic changes remains a challenge for population biologists (Hendry 2016; Janeiro et al.
418 2017). However, some models have been developed that try to predict when plasticity or
419 evolution might prevent the extinction of a population (Vedder, Bouwhuis, & Sheldon 2013;

420 Chevin & Lande 2010). A particularly important parameter is the additive genetic variance of
421 fitness. The additive genetic variance of fitness should be equivalent, in theory, to the rate of
422 adaptive genetic evolution (Bonnet, Morrissey, & Kruuk 2019; Fisher 1930; de Villemereuil et
423 al. 2016). Thus, comparison of the additive genetic variance of fitness might indicate how
424 quickly adaptive genetic evolution is occurring in wild versus captive populations. The goal of *ex*
425 *situ* populations is ultimately to directly support conservation efforts for wild populations, for
426 example through population augmentation. As such, *ex situ* and *in situ* partners should work
427 together to quantify the wild population as changes due to captivity will directly impact program
428 success, which is the intent of the OPA.

429 **Conclusions**

430 Integrated planning and management of wild and captive populations in an OPA can
431 improve the impact of conservation efforts for species at risk (Lees et al. 2021). Here, we present
432 and provide support for the argument that quantitative genetic analysis is a powerful tool that can
433 be used to enhance *ex situ* population management, and help to integrate *ex situ* and *in situ*
434 activities. Several examples exist demonstrating how phenotypes have come to differ between
435 captive and wild populations, despite best management practices for *ex situ* populations that
436 include efforts to reduce the loss of diversity. The consequences of these differences are not
437 always known, but, may impact the fitness of individuals that are used to directly support *in situ*
438 conservation efforts. Using existing pedigrees and phenotypic data in the Animal Model
439 approach, managers can disentangle the causes of these differences and understand their
440 consequences. By extending the approach to include genetic groups, analyses can also quantify
441 the effects of gene flow on phenotypes. Finally, these models can help managers to measure rates
442 of adaptation in captivity or predict whether captive populations are maintaining the adaptive

443 potential necessary to persist under changing conditions in the wild. Since the data to run
444 quantitative genetics analyses often already exists (*i.e.* in studbooks), we see quantitative genetic
445 analysis as a promising tool for conservation breeding that can likely be integrated with existing
446 management methods used for maintaining genetic diversity. In doing so, *ex situ* populations will
447 ensure they are as effective as possible in supporting *in situ* conservation efforts and managers
448 can better identify where to direct limited resources to answer questions critical to improving the
449 management of a species.

450 **Acknowledgements**

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

457 **References**

458 Aase, K., Jensen, H., & Muff, S. (2022). Genomic estimation of quantitative genetic parameters
459 in wild admixed populations. *Methods in Ecology and Evolution*, 13(5), 1014-1026. doi:

460 [10.1111/2041-210X.13810](https://doi.org/10.1111/2041-210X.13810)

461 Arnold, S.J., & Wade, M.J. (1984a). On the measurement of natural and sexual selection:

462 applications. *Evolution*, 38(4), 720-734. doi: 10.2307/2408384

463 Arnold, S.J., & Wade, M.J. (1984b). On the measurement of natural and sexual selection: theory.

464 *Evolution*, 38(4), 709-719. doi: 10.2307/2408383

465 Allegue, H., Araya-Ajoy, Y.G., Dingemanse, N.J., Dochtermann, N.A., Garamszegi, L.Z.,
466 Nakagawa, S., Réale, D., Schielzeth, H., & Westneat, D.F. (2017). Statistical quantification
467 of individual differences (SquID): an educational and statistical tool for understanding
468 multilevel phenotypic data in linear mixed models. *Methods in Ecology and Evolution*, 8(2),
469 257-267. doi: 10.1111/2041-210X.12659

470 Ballou, J.D., Lacy, R.C., & Pollak, J.P. (2020). PMx: Software for demographic and genetic
471 analysis and management of pedigreed populations (Version 1.6.2.20200110). Chicago
472 Zoological Society, Brookfield, Illinois, USA. Available from <http://www.scti.tools>

473 Baskett, M. L., Burgess, S. C., & Waples, R. S. (2013). Assessing strategies to minimize
474 unintended fitness consequences of aquaculture on wild populations. *Evolutionary
475 Applications*, 6(7), 1090–1108. doi:10.1111/eva.12089

476 Blumstein, D., Mari, M., Daniel, J., Ardron, J., Griffin, A., & Evans, C. (2006). Olfactory
477 predator recognition: wallabies may have to learn to be wary. *Animal Conservation*, 5(2),
478 87-93. doi: 10.1017/S1367943002002123

479 Bonamour, S., Chevin, L.-M., Charmantier, A., & Teplitsky, C. (2019). Phenotypic plasticity in
480 response to climate change: the importance of cue variation. *Philosophical Transactions of
481 the Royal Society of London. Series B, Biological Sciences*, 374(1768), 20180178.
482 doi:10.1098/rstb.2018.0178

483 Bonnet, T., Morrissey, M. B., & Kruuk, L. E. B. (2019). Estimation of Genetic Variance in
484 Fitness, and Inference of Adaptation, When Fitness Follows a Log-Normal Distribution.
485 *The Journal of Heredity*, 110(4), 383–395. doi: 10.1093/jhered/esz018

486 Bonnet, T., Morrissey, M., Clutton-Brock, T., Pemberton, J., & Kruuk, L. E. B. (2019). The role
487 of selection and evolution in changing parturition date in a red deer population. *PLoS*

488 *Biology*, 17(11), e3000493. doi: 10.1371/journal.pbio.3000493

489 Bonnet, T., Wandeler, P., Camenisch, G., & Postma, E. (2017). Bigger Is Fitter? Quantitative
490 Genetic Decomposition of Selection Reveals an Adaptive Evolutionary Decline of Body
491 Mass in a Wild Rodent Population. *PLoS Biology*, 15(1), e1002592. doi:
492 10.1371/journal.pbio.1002592

493 Byers, O., Lees, C., Wilcken, J., & Schwitzer, C. (2013). The One Plan Approach: The
494 philosophy and implementation of CBSG's approach to integrated species conservation
495 planning. *World association of Zoos and Aquariums Magazine*, 14, 2–5.

496 Chargé, R., Sorci, G., Saint Jalme, M., Lesobre, L., Hingrat, Y., Lacroix, F., & Teplitsky, C.
497 (2014). Does recognized genetic management in supportive breeding prevent genetic
498 changes in life-history traits? *Evolutionary Applications*, 7(5), 521–532.
499 doi:10.1111/eva.12150

500 Charmantier, A., Garant, D. D., & Kruuk, L. E. B. (2014). *Quantitative genetics in the wild*.
501 Oxford University Press, Oxford.

502 Charmantier, A., and Réale, D. (2005). How do misassigned paternities affect the estimation of
503 heritability in the wild? *Molecular Ecology* 14(9), 2839–2850.

504 Che-Castaldo, J. P., Grow, S. A., & Faust, L. J. (2018). Evaluating the contribution of North
505 American zoos and aquariums to endangered species recovery. *Scientific Reports*, 8(1),
506 9789. doi:0.1038/s41598-018-27806-2

507 Chevin, L.-M., & Lande, R. (2010). When do adaptive plasticity and genetic evolution prevent
508 extinction of a density-regulated population? *Evolution*, 64(4), 1143–1150.

509 doi:10.1111/j.1558-5646.2009.00875.x

510 Courtney Jones, S. K., Munn, A. J., & Byrne, P. G. (2018). Effect of captivity on morphology:
511 negligible changes in external morphology mask significant changes in internal
512 morphology. *Royal Society Open Science*, 5(5), 172470. doi:10.1098/rsos.172470

513 Cox, J.G., & Lima, S.L. (2006). Naiveté and an aquatic–terrestrial dichotomy in the effects of
514 introduced predators. *Trends in Ecology and Evolution*, 21(12), 674-680.
515 doi:10.1016/j.tree.2006.07.011

516 Dingemanse, N. J., & Dochtermann, N.A. (2013). Quantifying individual variation in behaviour:
517 mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54. doi:
518 10.1111/1365-2656.12013

519 English, S., Fawcett, T. W., Higginson, A. D., Trimmer, P. C., & Uller, T. (2016). Adaptive use
520 of information during growth can explain long-term effects of early life experiences. *The*
521 *American Naturalist*, 187(5), 620–632. doi:10.1086/685644

522 Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th ed.).
523 Harlow, Essex, UK: Longmans Green.

524 Faust, LJ, Bergstrom, YM, Thompson, SD, & Bier, L. 2019. PopLink Version 2.5. Lincoln Park
525 Zoo. Chicago, IL.

526 Firth, J.A., Hadfield, J.D., Santure, A.W., Slate, J., Sheldon, B.C. (2015). The influence of
527 nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees.
528 *Evolution*, 69(5), 1336-1344. doi:10.1111/j.1365-294X.2005.02619.x

529 Fischer, C. P., & Romero, M. L. (2020). Chronic captivity stress in wild animals is highly
530 species-specific. *Conservation Physiology*, 7(1), cozo93. doi:10.1093/conphys/cozo93

531 Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal
532 relocations. *Biological Conservation*, 96(1), 1–11. doi:10.1016/S0006-3207(00)00048-3

533 Fisher, D. N., Haines, J. A., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., & McAdam, A.
534 G. (2019). Indirect effects on fitness between individuals that have never met via an
535 extended phenotype. *Ecology Letters*, 22(4), 697–706. doi:10.1111/ele.13230

536 Fisher, D. N., & McAdam, A. G. (2019). Indirect genetic effects clarify how traits can evolve
537 even when fitness does not. *Evolution Letters*, 3(1), 4–14. doi:10.1002/evl3.98

538 Fisher, D. N., Wilson, A. J., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., ... McAdam,
539 A. G. (2019). Social effects of territorial neighbours on the timing of spring breeding in
540 North American red squirrels. *Journal of Evolutionary Biology*, 32(6), 559–571.
541 doi:10.1111/jeb.13437

542 Fisher, R. A. (1930). *The genetical theory of natural selection* (1st ed.). Oxford: Clarendon Press.

543 Frankham, R. (2008). Genetic adaptation to captivity in species conservation programs.
544 *Molecular Ecology*, 17(1), 325–333. doi:10.1111/j.1365-294X.2007.03399.x

545 Gaynor, R. C., Gorjanc, G., Hickey, J. M. (2021). AlphaSimR: an R package for breeding
546 program simulations. *G3*, 11(2), jkaa017. doi: 10.1093/g3journal/jkaa017

547 Gervais, L., Perrier, C., Bernard, M., Merlet, J., Pemberton, J.M., Pujol, B., & Quéméré, E.
548 (2019). RAD-sequencing for estimating genomic relatedness matrix-based heritability in the

549 wild: A case study in roe deer. *Molecular Ecology Resources*, 19(5), 1205-1217. doi:
550 10.1111/1755-0998.13031

551 Gienapp, P., & Brommer, J. E. (2014). Evolutionary dynamics in response to climate change. In
552 Quantitative genetics in the wild (pp. 254–273). Oxford University Press. Gienapp, P., Fior,
553 S., Guillaume, F., Lasky, J.R., Sork, V.L., & Csilléry, K. (2017). Genomic quantitative
554 genetics to study evolution in the wild. *Trends in Ecology & Evolution*, 32(12), 897-908.
555 doi: 10.1016/j.tree.2017.09.004

556 Griffin, A.S., Blumstein, D.T., & Evans, C.S. (2001). Training Captive-Bred or Translocated
557 Animals to Avoid Predators. *Conservation Biology* 14(5), 1317-1326. doi:10.1046/j.1523-
558 1739.2000.99326.

559 Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models:
560 The MCMCglmm R Package. *Journal of Statistical Software*, 33(2), 1–22.
561 doi:10.18637/jss.v033.i02

562 Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. B. (2010). The Misuse
563 of BLUP in Ecology and Evolution. *The American Naturalist*, 175(1), 116–125.
564 doi:10.1086/648604

565 Harbers, H., Neaux, D., Ortiz, K., Blanc, B., Laurens, F., Baly, I., ... Cucchi, T. (2020). The
566 mark of captivity: plastic responses in the ankle bone of a wild ungulate (*Sus scrofa*). *Royal*
567 *Society Open Science*, 7(3), 192039. doi:10.1098/rsos.192039

568 Henderson, C. R. (1950). Estimation of genetic parameters. In *Biometrics* (Vol. 6, pp. 186–187).
569 International Biometric Soc, Washington, DC.

570 Hendry, A. P. (2016). *Eco-evolutionary Dynamics* (1st ed.). Princeton, US: Princeton University
571 Press.

572 Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology.
573 *Behavioral Ecology*, 28(4), 948–952. doi:10.1093/beheco/ax023

574 Janeiro, M. J., Coltman, D. W., Festa-Bianchet, M., Pelletier, F., & Morrissey, M. B. (2017).
575 Towards robust evolutionary inference with integral projection models. *Journal of*
576 *Evolutionary Biology*, 30(2), 270–288. doi:10.1111/jeb.13000

577 Jolly, C. J., & Phillips, B. L. (2021). Rapid evolution in predator-free conservation havens and its
578 effects on endangered species recovery. *Conservation Biology*, 35(1), 383–385.
579 doi:10.1111/cobi.13521

580 Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the 'animal
581 model'. *Philosophical Transactions of the Royal Society of London. Series B*, 359(1446),
582 873–890. doi:10.1098/rstb.2003.1437

583 Lacy, R. C. (2012). Extending pedigree analysis for uncertain parentage and diverse breeding
584 systems. *The Journal of Heredity*, 103(2), 197–205. doi:10.1093/jhered/esr135

585 Lacy, R. C., Malo, A. F., & Alaks, G. (2018). Maintenance of genetic variation in quantitative
586 traits of a woodland rodent during generations of captive breeding. *Conservation Genetics*,
587 19(4), 789–802. doi:10.1007/s10592-018-1054-y

588 Lacy, R.C., & Pollak, J. P. (2021). *Vortex: A stochastic simulation of the extinction process*.
589 Version 10.5.5. Chicago Zoological Society, Brookfield, Illinois, USA.

590 Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters.
591 *Evolution*, 37(6), 1210-1226. doi:10.2307/2408842

592 Laskowski, K. L., Wolf, M., & Bierbach, D. (2016). The making of winners (and losers): how
593 early dominance interactions determine adult social structure in a clonal fish. *Proceedings*.
594 *Biological Sciences*, 283(1830), 1–6. doi:10.1098/rspb.2016.0183

595 Lees, C.M, Rutschman, A., Santure, A.W., & Beggs, J.R. 2021. Science-based, stakeholder-
596 inclusive and participatory conservation planning helps reverse the decline of threatened
597 species. *Biological Conservation* 260:109194

598 Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sunderland, MA:
599 Sinauer Associates.

600 Martin, J. G. A., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring individual
601 differences in reaction norms in field and experimental studies: a power analysis of random
602 regression models. *Methods in Ecology and Evolution*, 2(4), 362–374. doi:10.1111/j.2041-
603 210X.2010.00084.x

604 Meuwissen, T. H. E., Sonesson, A. K., Gebreyohans, G., & Wollims, J. A. (2020). Management
605 of genetic diversity in the era of genomics. *Frontiers in Genetics*, 11, 880. doi:
606 10.3389/fgene.2020.00880

607 McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal
608 temperament: causes and consequences of evolutionary change for captive, reintroduced,
609 and wild populations. *Animal Conservation*, 9(1), 39–48. doi:10.1111/j.1469-
610 1795.2005.00004.x

611 Mittell, E. A., Nakagawa, S., & Hadfield, J. D. (2015). Are molecular markers useful predictors
612 of adaptive potential? *Ecology Letters*, *18*(8), 772–778. doi:10.1111/ele.12454

613 Moiron, M., Araya-Ajoy, Y. G., Teplitsky, C., Bouwhuis, S., & Charmantier, A. (2020).
614 Understanding the social dynamics of breeding phenology: indirect genetic effects and
615 assortative mating in a long-distance migrant. *The American Naturalist*, *196*(5), 566–576.
616 doi:10.1086/711045

617 Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental
618 change. *Philosophical Transactions of the Royal Society of London. Series B, Biological*
619 *Sciences*, *363*(1497), 1635–1645. doi:10.1098/rstb.2007.0011

620 Monk, C. T., Bekkevold, D., Klefoth, T., Pagel, T., Palmer, M., & Arlinghaus, R. (2021). The
621 battle between harvest and natural selection creates small and shy fish: Natural vs. Harvest
622 Selection. *Proceedings of the National Academy of Sciences*, *118*(9), e2009451118. doi:
623 10.1073/pnas.2009451118.

624 Montgomery, M. E., Ballou, J. D., Nurthen, R. K., England, P. R., Briscoe, D. A., & Frankham,
625 R. (1997). Minimizing kinship in captive breeding programs. *Zoo Biology*, *16*(5), 377–389.
626 doi:10.1002/(SICI)1098-2361(1997)16:5<377::AID-ZOO1>3.0.CO;2-7

627 Morales-González, E., Fernández, J., Pong-Wong, R., Toro, M.A., Villanueva, B. (2021).
628 Changes in allele frequencies when different genomic coancestry matrices are used for
629 maintaining genetic diversity. *Genes*, *12*(5), 673. doi: 10.3390/genes12050673

630 Morrissey, M.B., & Wilson, A.J. (2010). pedantics: an r package for pedigree-based genetic
631 simulation and pedigree manipulation, characterization and viewing. *Molecular Ecology*

632 *Resources*, 10(4), 711–719. doi: 10.1111/j.1755-0998.2009.02817.x

633 Moseby, K., Cameron, A., & Crisp, H. A. (2013). Can predator avoidance training improve
634 reintroduction outcomes for the greater bilby in arid Australia? *Animal Behaviour*, 83(4),
635 1011-1021. doi: 10.1016/j.anbehav.2012.01.023

636 Muff, S., Niskanen, A. K., Saatoglu, D., Keller, L. F., & Jensen, H. (2019). Animal models with
637 group-specific additive genetic variances: extending genetic group models. *Genetics*,
638 *Selection, Evolution*, 51(1). doi:10.1186/s12711-019-0449-7

639 Munch, K. L., Noble, D. W. A., Budd, L., Row, A., Wapstra, E., & While, G. M. (2018).
640 Maternal presence facilitates plasticity in offspring behavior: insights into the evolution of
641 parental care. *Behavioral Ecology*, 29(6), 1298–1306. doi:10.1093/beheco/ary122

642 Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual
643 phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, 20, 831–844.
644 doi:10.1111/j.1420-9101.2007.01300.x

645 O'Regan, H. J., & Kitchener, A. C. (2005). The effects of captivity on the morphology of captive,
646 domesticated and feral mammals. *Mammal Review*, 35(3-4), 215–230. doi: 10.1111/j.1365-
647 2907.2005.00070.x

648 Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual*
649 *Review of Ecology, Evolution, and Systematics*, 37(1), 637–669.
650 doi:10.1146/annurev.ecolsys.37.091305.110100

651 Pelletier, F., Réale, D., Watters, J., Boakes, E. H., & Garant, D. (2009). Value of captive

652 populations for quantitative genetics research. *Trends in Ecology & Evolution*, 24(5), 263–
653 270. doi:10.1016/j.tree.2008.11.013

654 Pigeon, G., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Intense selective hunting
655 leads to artificial evolution in horn size. *Evolutionary Applications*, 9(4), 521–530.
656 doi:10.1111/eva.12358

657 Ponzi, E., Keller, L. F., Bonnet, T., & Muff, S. (2018). Heritability, selection, and the response to
658 selection in the presence of phenotypic measurement error: Effects, cures, and the role of
659 repeated measurements. *Evolution*, 72(10), 1992–2004. doi:10.1111/evo.13573

660 Postma, E. (2006). Implications of the difference between true and predicted breeding values for
661 the study of natural selection and micro-evolution. *Journal of Evolutionary Biology*, 19(2),
662 309–320. doi:10.1111/j.1420-9101.2005.01007.x

663 Power, M. L., Oftedal, O. T., & Tardif, S. D. (2002). Does the milk of Callitrichid monkeys
664 differ from that of larger anthropoids? *American Journal of Primatology*, 56(2), 117–127.
665 Retrieved from <https://doi.org/10.1002/ajp.1068>

666 Power, M. L., Verona, C. E., Ruiz-Miranda, C., & Oftedal, O. T. (2008). The composition of
667 milk from free-living common marmosets (*Callithrix jacchus*) in Brazil. *American Journal*
668 *of Primatology*, 70(1), 78–83. doi:10.1002/ajp.20459

669 Price, G. R. (1970). Selection and Covariance. *Nature*, 227(5257), 520–521.
670 doi:10.1038/227520a0

671 Princée, F. P. G. (2016). Exploring studbooks for wildlife management and conservation.

672 Springer International Publishing, East Rudham, Norfolk, UK.

673 Queller, D. C. (2017). Fundamental Theorems of Evolution. *The American Naturalist*, 189(4).
674 doi:10.1086/690937

675 Ralls, K., Ballou, J.D., Rideout, B.A., & Frankham, R. (2000). Genetic management of
676 chondrodystrophy in California condors. *Animal Conservation*, 3(2), 145-153. doi:
677 10.1111/j.1469-1795.2000.tb00239.x

678 Reading, R.P., Miller, B., and Shepherdson, D. (2013). The value of enrichment to reintroduction
679 success. *Zoo Biology*, 32(3), 332-341. doi: 10.1002/zoo.21054

680 Reed, D. H., & Frankham, R. (2001). How closely correlated are molecular and quantitative
681 measures of genetic variation? A meta-analysis. *Evolution*, 55(6), 1095–1103.
682 doi:10.1111/j.0014-3820.2001.tb00629.x

683 Reid, J. M., Arcese, P., Nietlisbach, P., Wolak, M. E., Muff, S., Dickel, L., & Keller, L. F.
684 (2020). Immigration counter-acts local micro-evolution of a major fitness component:
685 Migration-selection balance in free-living song sparrows. *Evolution Letters*, 5(1), 48–60.
686 doi:10.1002/evl3.214

687 Rendel, J.M., & Robertson, A. (1950). Estimation of genetic gain in milk yield by selection in a
688 closed herd of dairy cattle. *Journal of Genetics*, 50(1), 1-8. doi: 10.1007/BF02986789

689 Saura, M., Pérez-Figueroa, A., Fernández, J., Toro, M. A., Caballero, A. (2008). Preserving
690 population allele frequencies in ex situ conservation programs. *Conservation Biology*,
691 22(5), 1277-1287. doi: 10.1111/j.1523-1739.2008.00992.x

692 Schulte-Hostedde, A. I., & Mastromonaco, G. F. (2015). Integrating evolution in the
693 management of captive zoo populations. *Evolutionary Applications*, 8(5), 413.
694 doi:10.1111/eva.12258

695 Soorae, P.S. (ed). 2021. Global conservation translocation perspectives: 2021. Case studies from
696 around the globe. IUCN SSC Conservation Translocation Specialist Group, Environment
697 Agency - Abu Dhabi and Calgary Zoo, Canada.

698 Sultan, S. E. (2015). *Organism and Environment*. Oxford University Press.

699 Sundström, L. F., Löhmus, M., & Devlin, R. H. (2016). Gene—environment interactions
700 influence feeding and anti-predator behavior in wild and transgenic coho
701 salmon. *Ecological Applications*, 26(1), 67–76. <http://www.jstor.org/stable/24701221>

702 Tardif, S. D., Power, M. L., Ross, C. N., & Rutherford, J. N. (2013). Body mass growth in
703 common marmosets: toward a model of pediatric obesity. *American Journal of Physical*
704 *Anthropology*, 150(1), 21–28. doi:10.1002/ajpa.22110

705 Tavecchia, G., Viedma, C., Martínez-Abraín, A., Bartolomé, M.-A., Gómez, J. A., & Oro, D.
706 (2009). Maximizing reintroduction success: Assessing the immediate cost of release in a
707 threatened waterfowl. *Biological Conservation*, 142(12), 3005–3012.
708 doi:doi.org/10.1016/j.biocon.2009.07.035

709 Thomson, C. E., Winney, I. S., Salles, O. C., & Pujol, B. (2018). A guide to using a multiple-
710 matrix animal model to disentangle genetic and non-genetic causes of phenotypic variance.
711 *PloS One*, 13(10), e0197720. doi:10.1371/journal.pone.0197720

712 United Nations Environment Program Convention on Biological Diversity (2010) Montréal,
713 UNEP/CBD/COP/DEC/X/2. <https://www.cbd.int/decision/cop/?id=12268>

714 Vedder, O., Bouwhuis, S., & Sheldon, B. C. (2013). Quantitative assessment of the importance
715 of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS*
716 *Biology*, *11*(7), 1–10. doi:10.1371/journal.pbio.1001605

717 de Villemereuil, P., Schielzeth, H., Nakagawa, S., & Morrissey, M. (2016). General methods for
718 evolutionary quantitative genetic inference from generalized mixed models. *Genetics*,
719 *204*(3), 1281-1294. doi:10.1534/genetics.115.186536

720 Wade, M. J., & Goodnight, C. J. (1998). Perspective: The theories of Fisher and Wright in the
721 context of metapopulations: when nature does many small experiments. *Evolution*, *52*(6),
722 1537–1553. doi:10.1111/j.1558-5646.1998.tb02235.x

723 Walsh, B., & Lynch, M. (2018). *Evolution and Selection of Quantitative Traits*. Oxford, New
724 York: Oxford University Press.

725 West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

726 Williams, S.E., & Hoffman, E.A. (2009). Minimizing genetic adaptation in captive breeding
727 programs: A review. *Biological Conservation*, *142*(11), 2388-2400.
728 doi:10.1016/j.biocon.2009.05.034

729 Willoughby, J.R., Fernandez, N.B., Lamb, M.C., Ivy, J.A., Lacy, R.C., & DeWoody, J.A. (2015).
730 The impacts of inbreeding, drift and selection on genetic diversity in captive breeding
731 populations. *Molecular Ecology*, *24*(1), 98-110. doi:10.1111/mec.13020

- 732 Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk,
733 L. E. B., Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal*
734 *Ecology*, 79(1), 13–26. doi:10.1111/j.1365-2656.2009.01639.x
- 735 Wolak, M. E. (2012). Nativ: An R package to create relatedness matrices for estimating non-
736 additive genetic variances in animal models. *Methods in Ecology and Evolution*, 3(5), 792–
737 796. doi:10.1111/j.2041-210X.2012.00213.x
- 738 Wolak, M. E., & Keller, L. F. (2014). Dominance genetic variance and inbreeding in natural
739 populations. In *Quantitative genetics in the wild* (pp. 104–127). Oxford University Press.
- 740 Wolak, M. E., & Reid, J. M. (2017). Accounting for genetic differences among unknown parents
741 in microevolutionary studies: how to include genetic groups in quantitative genetic animal
742 models. *Journal of Animal Ecology*, 86(1), 7–20. doi:10.1111/1365-2656.12597

743

744

745

746

747

748 **Figure Captions**

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

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

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

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

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

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

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

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

777

778

779

780

781

782

783

784

785

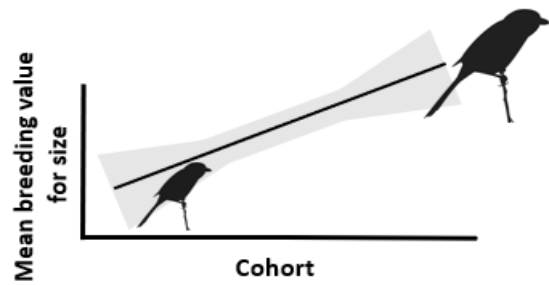
786

787

788 **Figures**

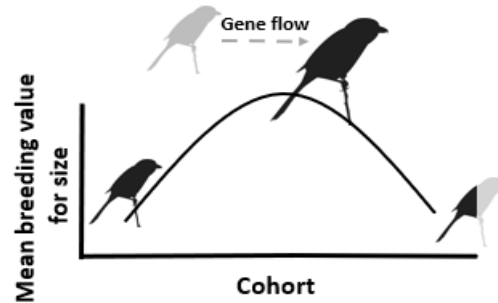
Are there signs of evolution in captivity or the wild?

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



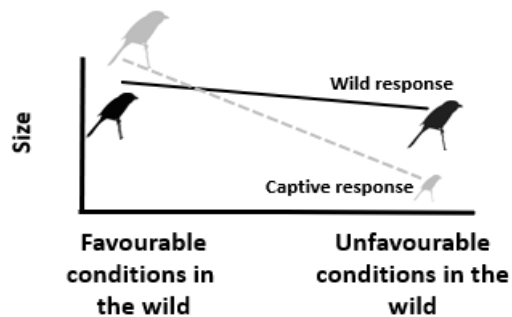
Does gene flow affect wild or captive phenotypes?

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



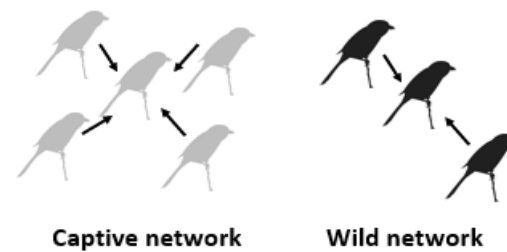
Does captivity alter plastic responses?

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)



789

790 **Fig. 1**

791

792

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 Plasticity

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 MCMCgllmm.
- 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

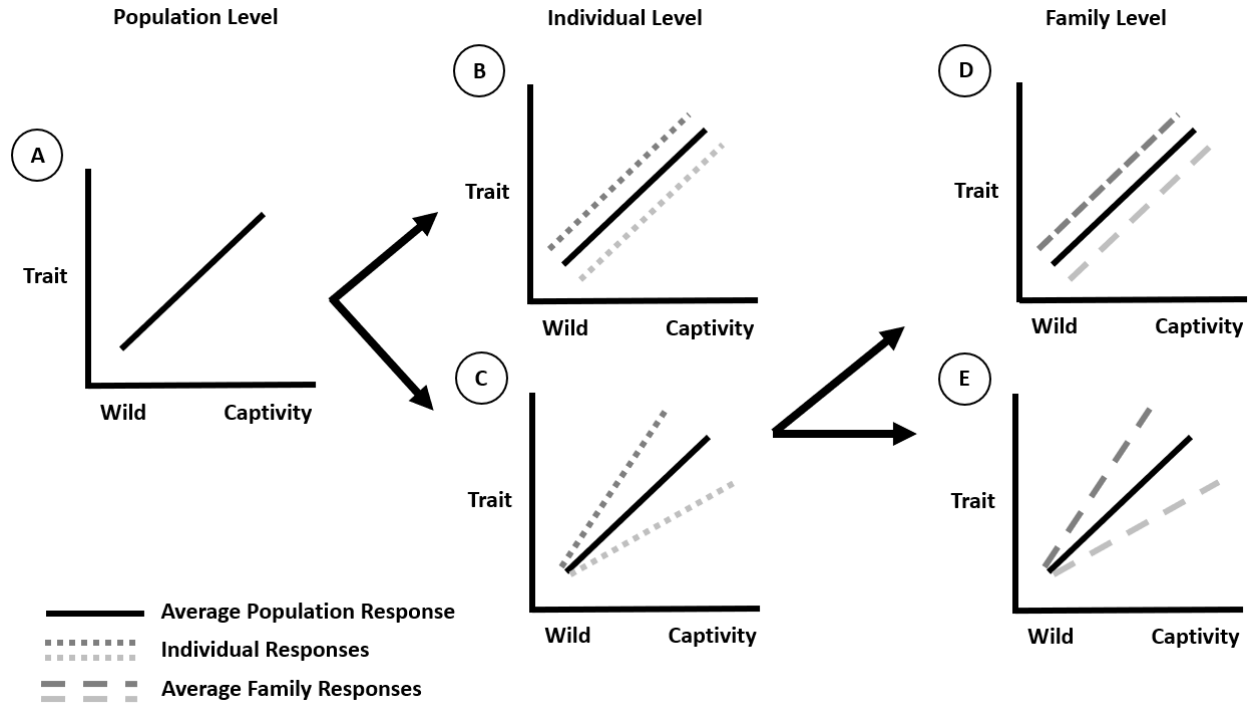
Differences in social networks over time and between wild and captive environments might contribute to phenotypic changes observed.

- 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)

793

794

Fig. 2



795

796 **Fig. 3**

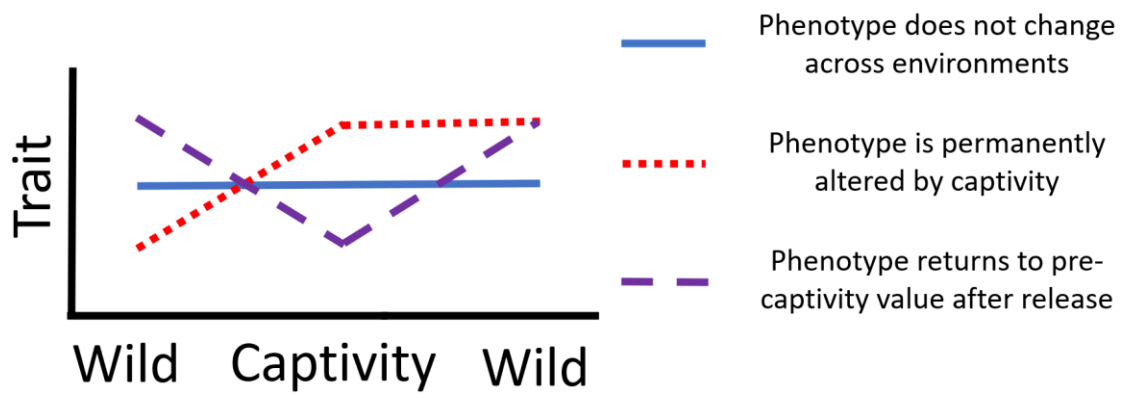
797

798

799

800

801



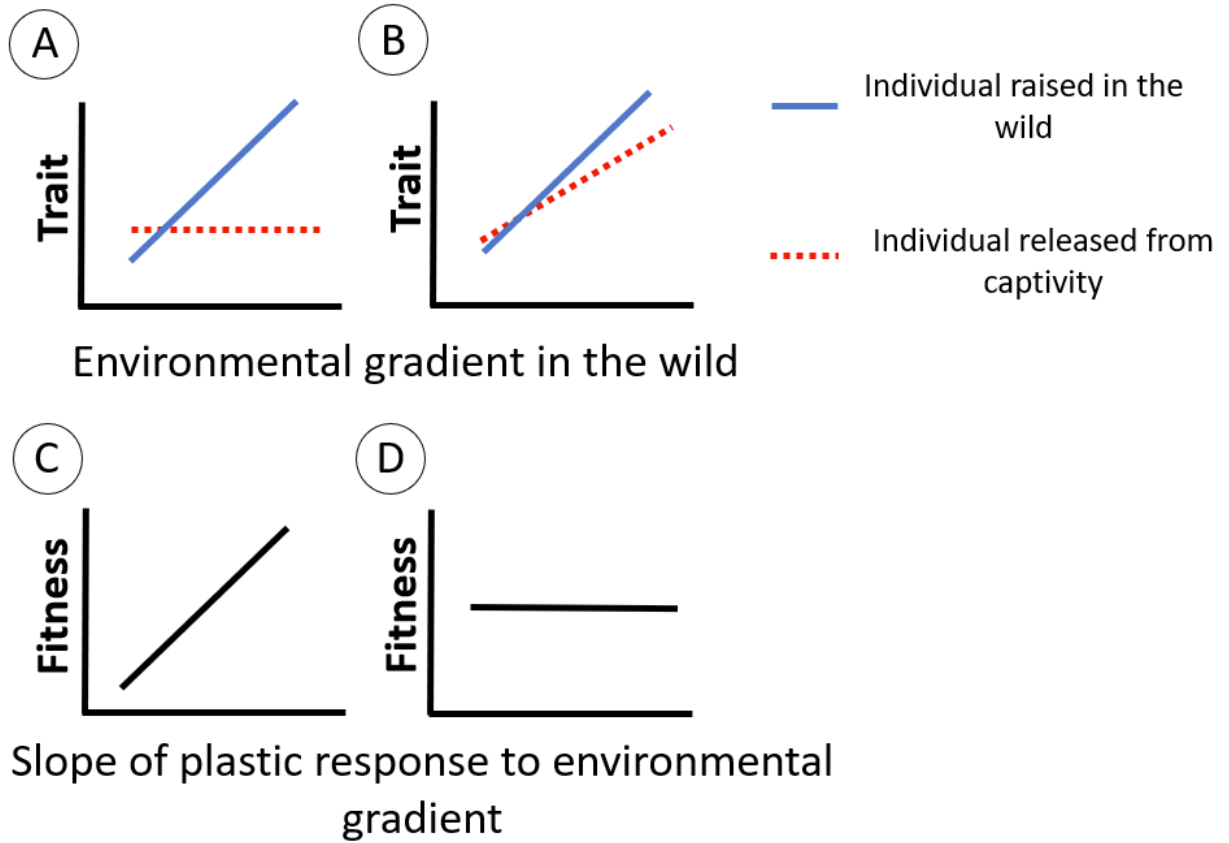
802 **Fig. 4**

803

804

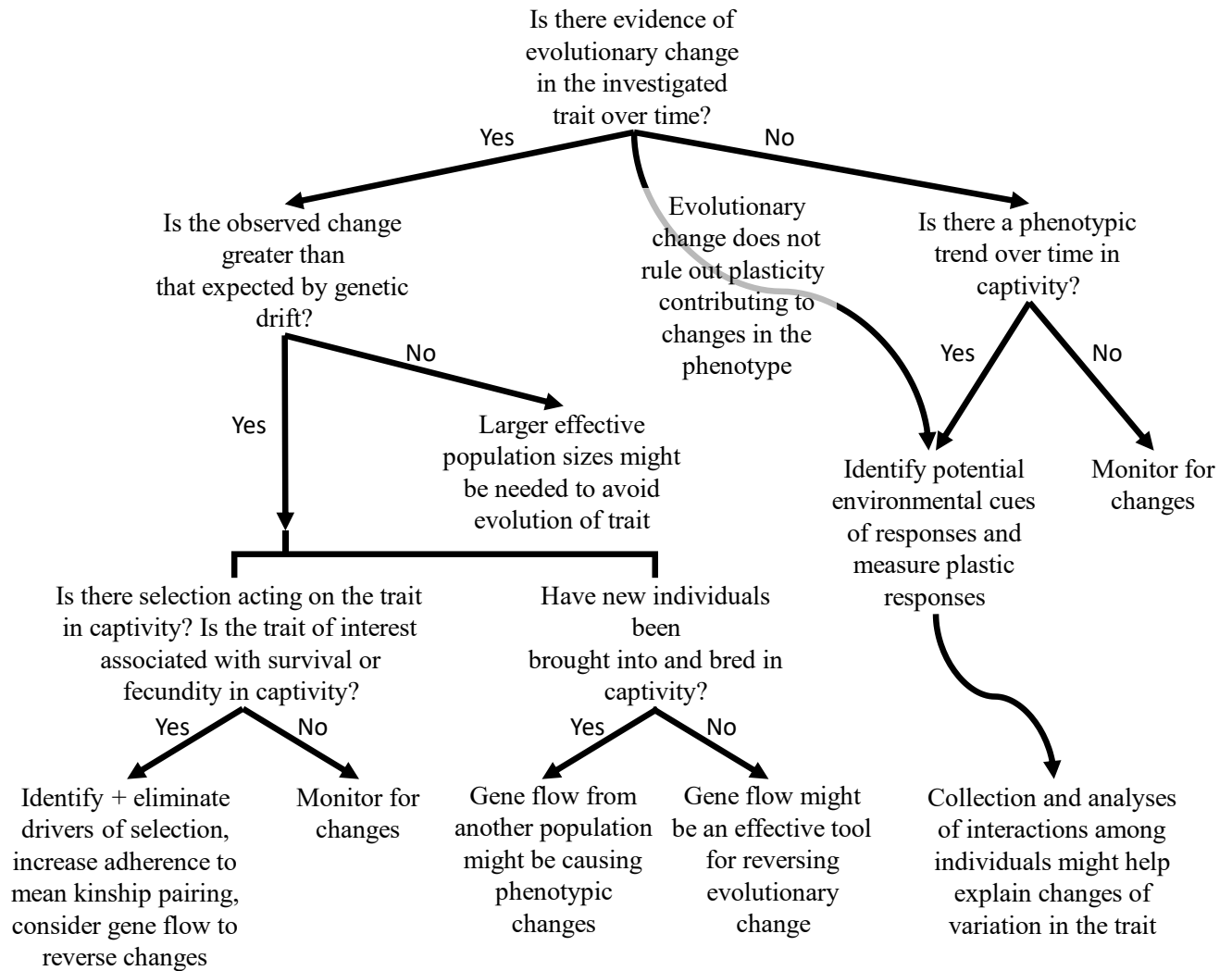
805

806



807

808 Fig. 5



809

810 **Fig. 6**

811