



Quantitative genetics for a more qualitative conservation

Peter Galbusera based on peer reviews by **Timothée Bonnet** and 1 anonymous reviewer

Drew Sauve, Jane Hudecki, Jessica Steiner, Hazel Wheeler, Colleen Lynch, Amy A. Chabot (2022) Improving species conservation plans under IUCN's One Plan Approach using quantitative genetic methods. *EcoEvoRxiv*, ver. 9, peer-reviewed and recommended by Peer Community in Zoology. <https://doi.org/10.32942/osf.io/n3zxp>

Submitted: 21 February 2022, Recommended: 25 August 2022

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Genetic (bio)diversity is one of three recognised levels of biodiversity, besides species and ecosystem diversity. Its importance for species survival and adaptation is increasingly highlighted and its monitoring recommended (e.g. O'Brien et al 2022). Especially the management of ex-situ populations has a long history of taking into account genetic aspects (through pedigree analysis but increasingly also by applying molecular tools). As in-situ and ex-situ efforts are nowadays often aligned (in a One-Plan-Approach), genetic management is becoming more the standard (supported by quickly developing genomic techniques). However, rarely quantitative genetic aspects are raised in this issue, while its relevance cannot be underestimated. Hence, the current manuscript by Sauve et al (2022) is a welcome contribution, in order to improve conservation efforts. The authors give a clear overview on how quantitative genetic analysis can aid the measurement, monitoring, prediction and management of adaptive genetic variation. The main tools are pedigrees (mainly of ex-situ populations) and the Animal Model. The main goal is to prevent adaptation to captivity and altered genetics in general (in reintroduction projects). The confounding factors to take into account (like inbreeding, population structure, differences between facilities, sample size and parental/social effects) are well described by the authors. As such, I fully recommend this manuscript for publication, hoping increased interest in quantitative analysis will benefit the quality of species conservation management.

References:

O'Brien D, Laikre L, Hoban S, Bruford MW et al. (2022) Bringing together approaches to reporting on within species genetic diversity. *Journal of Applied Ecology*, 00, 1–7. <https://doi/10.1111/1365-2664.14225>

Sauve D., Spero J., Steiner J., Wheeler H., Lynch C., Chabot A.A. (2022) Improving species conservation plans under IUCN's One Plan Approach using quantitative genetic methods. EcoEvoRxiv, ver. 9 peer-reviewed and recommended by Peer Community in Zoology.
<https://doi.org/10.32942/osf.io/n3zxp>

Reviews

Evaluation round #3

DOI or URL of the preprint: <https://doi.org/10.32942/osf.io/n3zxp>
Version of the preprint: v7

Authors' reply, 20 July 2022

Thank you we have now made the suggested edits in the abstract and to Figure 3.

Best,
Drew

Decision by **Peter Galbusera**, posted 15 July 2022

accept with minor comments

Thank you for the fast reply.
Good to see all comments have been addressed.
Two small editorial comments remain:
L. 18 (abstract) "However, it is difficult..."
Fig 3: change "phenotypic level" into "individual level"

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.32942/osf.io/n3zxp>
Version of the preprint: v6

Authors' reply, 14 July 2022

Dear Peter Galbusera,

Thank you for your helpful suggestions and guidance on the peer review/recommendation process. We have attached information on our updated preprint and uploaded our responses to your suggestions and the suggestions from Reviewer #2.

Sincerely,
Drew Sauve (on behalf of all coauthors)
[Download author's reply](#)

Decision by Peter Galbusera, posted 13 July 2022

accept with minor comments

Both reviewers are recommending to accept the revised (v6) version of the manuscript. One reviewer has some minor comments that should be addressed though.

As subject editor I hence recommend to accept the manuscript with minor comments. I have added some (editorial) comments below. These are of course open for discussion. The manuscript will not be resent to the reviewers though.

Minor comments:

Abstract: Currently lack a sentence describing the problem. So, please, mention how phenotypic changes (e.g. due to genetic adaptation to captivity) can be a problem for e.g. reintroductions.

Main text:

L. 65: change "... based on matching mean kinship" into "based on mean kinship and inbreeding avoidance..."

L. 91: "...integration of..."

L. 98: "... in the wild, in reintroduction programs."

L.125: "As one of the goals is..." (besides research and educational/fundraising goals)

L. 172: ". However,..."

L. 177: "... variance is due to different..."

L. 399: change into "best practices based on mean kinship pairing and inbreeding avoidance".

L. 535: change "both" into "also"?

L. 756: remove "genetic"

L. 792 (Fig 3): change "phenotypic level" into "individual level"; it is also not clear why there are two parallel lines at the family level and why these purple 'family' lines are parallel if there are differences between families (situation E). I guess the purple lines are NOT specific for families but that is not clear from the legend. I suggest to keep the solid black line specific for the population level, dotted lines for the individual level and striped lines for the family level. Different individuals (and families) can then be symbolized by different colors (but not black).

Reviewed by anonymous reviewer 1, 12 July 2022

Mainly satisfied with the modifications to the manuscript which have fulfilled my previous comments. Argumentation is now clearer and more precise. The only point where I have still some concerns is related to the ambiguity regarding the citation of the classical management methodology currently being applied in ex-situ conservation programs. In several places of the manuscript (e.g., line 65 or line 399) the expression 'mate-pairing based on kinships' seems to mean that minimisation of the kinship (coancestry) is only used to decide the mating scheme to limit the rise of inbreeding when, actually, this parameter is also to be accounted in the selection process itself, determining the 'redundant' individuals or the ones belonging to underrepresented lineages which should be promoted to produce offspring (maintenance of the genetic diversity).

Additionally, I detected a couple of typos:

- Line 91: ' ... integration **OF** quantitative ...'
- Line 177: Something missing between 'variance' and 'different'. Suggestion: ' ... **is due to** ...' or something similar.

Reviewed by [Timothée Bonnet](#), 12 July 2022

This is the second time I review this manuscript. I think the authors edited the manuscript appropriately in response to the first round of reviews and I do not have any more comments. I think this manuscript should now be recommended and that it will be a very useful addition to the literature on ex-situ conservation (and also a nice review of quantitative genetic methods for wildlife more in general).

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.32942/osf.io/n3zxp>

Authors' reply, 21 June 2022

Dear Peter Galbusera,

We appreciate the thoughtful and constructive comments from Timothée Bonnet and Jesús Fernández Martín

Please find attached our revised manuscript with tracked changes as well as our replies to each of the reviewer's comments in a table format. We have uploaded a new preprint to the EcoEvoRxiv server and the preprint is listed as version 6.

Thank you for your consideration,

Drew

[Download author's reply](#)

[Download tracked changes file](#)

Decision by [Peter Galbusera](#), posted 19 April 2022

major revisions required

Based on the extensive reports of the two reviewers, I encourage the authors to submit a revised manuscript taking into account (and responding to) all comments by the reviewers. Both are, in general, in favor of the manuscript but clearly request several clarifications, corrections and additions. Furthermore, the manuscript seems to need additional editing efforts in terms of avoiding redundancies and correct references to literature and figures. Overall I think that such a revised manuscript has the potential to become a scientific paper of interest to researchers as well as managers involved in species conservation. The resubmitted manuscript will be subject to a new round of review.

Reviewed by [Timothée Bonnet](#), 25 March 2022

The manuscript reviews questions that can be addressed with quantitative genetic methods in ex-situ populations and how they could be relevant to conservation.

This work is timely given the large number of conservation programs involving ex-situ populations and the increasing ease to estimate relatedness in a population (and therefore apply quantitative genetic methods). There is an untapped trove of well monitored ex-situ populations for which quantitative genetics could assist conservation and reveal interesting biology too.

The review of methods and questions is quite comprehensive and should be useful beyond research in conservation involving ex-situ populations, for anyone wanting an overview of quantitative genetic methods for wild organisms.

The manuscript is well written and clear. I have comments that may require a bit of work, but nothing that should be difficult or long to achieve.

L.99 In addition to phenotypic plasticity and evolutionary change I like to consider changes in the demographic structure for instance changes in the distribution of age, sex or stage classes in the population. Demographic structure is sometimes seen as a component of phenotypic plasticity, or more often seen as a simple confounder to be corrected for in quantitative genetic studies. Changes in the demographic structure seem quite likely when a population is taken from the wild to live ex-situ, so it has the potential to explain phenotypic changes (which you may or may not expect would be reversed if the population is reintroduced into the wild). Therefore I think it would be good to consider demographic structure explicitly (not just as a confounder) in the context of the article.

L.122-124 You may add other possible important consequences: altered ecological role of the organism, or mismatch between the properties of the organism and societal expectations.

L.139 After a paragraph on molecular genetic variation, I was confused by the end "through monitoring of both genetic and phenotypic variation". You should be more specific / conceptually consistent. On the one hand there is a contrast between (quantitative) genetic vs. phenotypic variation (phenotypic variation being caused by genetic and non-genetic variation). On the other hand there is a contrast between molecular genetic variation vs. quantitative genetic variation, with quantitative genetic variation being phenotypic variation ascribed to (molecular) genetic variation.

L.145 To use quantitative genetic methods you don't necessarily need a pedigree. Instead, you need a way to estimate pairwise additive relatedness. That can be done using a pedigree, partial information on kinship, or molecular markers (e.g., GRM computed from SNPs).

L.183 Maybe clarify to "[reduced] genetic variation and [increased] inbreeding" ?

L.191-196 Managers could also use estimated breeding values to drive change in breeding values in the desired direction through selective breeding.

L.199-200 Statistical power will also depend on the structure of the pedigree and its covariation with confounding variables (e.g., maternal effects).

L.204-206 Maybe I am missing the point, but isn't it trivial to document a change in average phenotype? If you cannot infer the causes of the change I am not sure it is really useful (for reasons you highlighted above: the phenotypic trend may be the result of different genetic changes and environmental changes.)

L.234 Isn't the section more about "Changes in plasticity" rather than "changes caused by plasticity" ?

L.251-252 I am not sure that it true. If you could show that an environmental variable *causes* a change in the mean value of a trait expressed only once in life, wouldn't you say that you have inferred a plastic response? That being said, I agree that it is often easier to study the plasticity of traits expressed multiple time in life.

L.263-271 I am no expert, but I think there are some good examples of anti-predation behaviours that can be lost in captivity and hard to re-learn in introduced population. Maybe a good example to give here.

L.289-293 Maybe clarify what is the output of the SQuID and why it is relevant in this context?

Box 1 L.4 I am not sure the intercept indicates the average trait value. Isn't it the case only if the environmental variable is mean-centered?

L.351-353 3 spaces are missing: "value.Studbooks", "events.generate" and "tables.to".

L.405 I may have written the interpretation of additive genetic variance in fitness wrong somewhere, but a more accurate statement would be "the rate of genetic evolution [due to selection]" or "the rate of [adaptive] genetic evolution".

L.407 again, "how quickly [adaptive] genetic evolution".

L.696 Don't you want some caption for figure 2?

Figure 3: I don't understand how (D) is supposed to illustrate a subcase of (C). To me it looks like all families in (D) have the same plastic response and differ only in elevation, whereas (C) illustrated differences in plastic responses.

L.709 Shouldn't it be "Figure 5" instead of "Fig 4" ?

Timothée Bonnet (I sign all my reviews)

Reviewed by anonymous reviewer 1, 13 April 2022

Improving species conservation plans under IUCN's One Plan Approach using quantitative genetic methods, by Sauve and coworkers. The authors review the aspects that have to be taken into account when managing exsitu conservation programs regarding the coordination with the wild populations. They also comment on the methods (especially quantitative genetics) available to be implemented. I find this study very useful to rise the concern on the stakeholders that conservation cannot be split into insitu and exsitu actions but have to deal with the population as a whole and coordinate aims and methods with the final goal of guaranteeing stable and far-from-risk populations in the wild (the known as One Plan Approach). In this regard, I think this is a timely and needed exercise.

Simplifying a bit, or being pragmatic, the required change of paradigm in the management of (ex)itu conservation populations is to go beyond the classical idea of maintaining general (neutral) genetic diversity and including adaptive variation into the goals and criteria. Obviously, if we maintain plenty of general genetic variation, hopefully also adaptive variation will remain (drift affects the whole genome). However, if there is information on genetic conformation for fitness-related traits the probability of survival of the population will be higher by including it into the management procedures. The new philosophy would be performing some kind of 'selection' for key traits while maintaining general genetic diversity. This is the objective of the Optimal Contribution (OC) theory (Meuwissen 1997, *J. Anim. Sci.* and posterior developments) that it is common in breeding programs of commercial populations. This OC could be mentioned in the paper to widen the methodological options for managers. Actually, fitness is already accounted for in the management of conservation programs when (mono)genetic defects appear by avoiding the use of carriers of the deleterious allele. The new situation implies dealing with more or less infinitesimal traits and, thus, the need of applying quantitative genetics methods.

A large amount of the submitted text is devoted to the relevant problem of plasticity. However, I think that in the manuscript plasticity is mixed and somehow confounded with GxE interaction. The latter is related with adaptation to captivity (even if both environments are stable) as the relative performance between genotypes may be different in captivity and the wild and, in the extreme, the best fitted genotype exsitu has a poor performance in the wild. GxE interaction can be dealt with more easily by performing multitrait evaluations (phenotype in captivity and nature considered different traits). Then captive individuals can be evaluated for their expected performance in the wild and used as parents of the next generation (or not). No need to measure the same individual in captivity and the wild but having relatives in both environments. For example, a parent can be evaluated by their released offspring.

Contrarily, detecting the effects of captivity on the plasticity of individuals would imply a greater sampling/recording effort. The feasibility of the use of plasticity as a criterion should be critically included in the manuscript. For example: how to determine the key traits for adaptation/plasticity in the wild? What are the required sampling sizes to obtain enough accuracies? In the end, everything is related to the importance of planning the captivity environment to minimise the differences with the wild (and to what extent this is possible).

Anyway, in the absence of further information, aiming at neutral variation minimises drift, the changes in allelic frequencies and the adaptation to captivity. Thus, it is not as bad as implicit in some of the comments in the text.

The study would benefit from the inclusion of a (brief) discussion on the extra advantages that molecular information could provide to the One Plan Approach management. For example (but not limited): i) determining founder relationships in exsitu populations; ii) trace lineages from released individuals (descendants of reintroduced); iii) detect genomic regions involved in adaptation (differences between wild and captive populations).

I would also want to point out to a problem on the format of the manuscript. Throughout the manuscript plenty of redundancies can be found, with the same idea presented several times. This enlarge (unnecessary) the text and makes the reading more tiring.

Further comments follow:

- Lines 44-45: I would include in the list those captive populations created in specific centres (i.e. for single species) not fitting the traditional definition of zoos. I think that such populations offer more opportunities for the management and more powerful actions can be conducted.

- Line 51: I think you should be more precise with the expression 'the potential for reduced reproductive fitness' when listing the challenges in the management of ex situ populations by highlighting that you mean the failure to reproduce in the wild once released (adaptation to captivity). Because, in general, ex situ populations perform reproductively well, mainly due to the benign environment. Moreover, as the next part of the sentence says 'adaptation to captivity' it may lead to think that they are different factors. If you mean loss of fitness due to inbreeding depression, I think that the problem of inbreeding is usually worse in the wild than in (well) managed ex situ populations.

- Line 65: This citation is missing in the References section.

- Line 70: The concept of 'realities' could be a bit expanded commenting on the conflict optimal vs. feasible as well as the problem of the expected vs. the observed outcomes. The latter sometimes arises because of some factors not accounted leading to evolutionary changes (line 72) due to unintentional selection (line 74).

- Lines 75-76: This is what I expressed in my general comments. Not only neutral unspecific diversity should be preserved by minimising coancestry, but also data on adaptive diversity should be included in the management criteria.

- Line 94: There is no Section 6. There is a mismatch between number of sections and the description of the contents.

- Line 156: The average breeding value is a parameter of a trait, not of a phenotype.

- Line 164: Avoiding evolutionary change can be pursued by controlling the breeding values for specific traits or, in a general way, by minimising the changes in the genetic makeup due to drift. Saura et al. (Cons. Genet. 2008) already proved that minimising coancestry (even from pedigree information) lead to the smallest change in allelic frequencies. More recently, different authors (Meuwissen et al. 2000, Front. Genet., Morales-González et al. 2021, Genes) explored the effects on the change of allelic frequencies from the use of different molecular coancestry matrices in the management of conservation programs.

- Lines 182-183: This sentence is a bit misleading due to the expression 'contribute'. I think that something like 'affect' or 'has a great influence in the performance for important traits'. Moreover, this is also true for large populations, at least for the part of the genetic variation.

- Lines 195-196: I find this sentence a bit 'speculative' because in practical terms new captures to be included in ex situ populations are mainly opportunistic. It is quite difficult to pick up the individual with the required neutral variation to enlarge the genetic background of the population and it may be even harder to detect the one with the 'appropriate' breeding value.

- Lines 208-209: Please, rewrite the definition of Animal Model; it seems that all individuals have to be founders with not known ancestors to apply this methodology. Additionally, there are developments of Animal Model methodology that allows for the several populations, for example in crossbreeding selection schemes where not only (additive) breeding values can be estimated but also dominant effects calculated and accounted for.

- Line 212 and followings: And alternative for the genetic groups is the use of molecular information in a punctual way to estimate the genetic relationships between founders or to apply the concept of 'metafounders' in the evaluation of the genetic merit.

- Lines 218-219: The original idea of the concept of 'genetic groups' was to account for the fact that different founders might come from different populations (with different genetic backgrounds). For example when a single captive population is constructed by sampling individuals from several isolated regions. If new captures occurs in the same original population a not much different background is expected (in general) as to consider that is a different genetic group. Moreover, when is time to change to a new group? Two generations? Five?

- Lines 220-221: This feature is not (completely) related to the definition or not of genetic groups. Even if all

founders are assumed to be from the same group, the proportion of insitu (founders' contribution) and exsitu (non-founders' contribution) influence in the genome can be calculated from the pedigree and monitored.

- Line 265: Replace 'a' by a comma.
- Line 265: From this moment it seems that all references to figures are wrong. Here it should be Fig. 4 instead Fig. 3, shouldn't it?
- Line 292: As said before, I find quite difficult to detect plasticity but detect differences in genetic conformation by evaluating the differences in phenotype (Animal Model).
- Line 299: There is a missing 'of' between 'impacts' and 'captivity'.
- Line 308: I agree with the authors that differences in social interactions between exsitu and insitu populations are crucial to determine the success of reintroductions. At the same time I think it is the most difficult aspect to be accounted for when 'naturalising' the captive environment.
- Line 318: In most captive breeding programs hand-reared animals are never used for reintroductions.
- Line 320: The correct spelling is *Callithrix* (missing 'i').
- Lines 335-336: Not very informative on what you will find in this section. It is plenty of lines on software.
- Line 339: Missing 'in' between 'maintained' and 'a variety'.
- Lines 342-343: Rewrite to avoid the use of 'options' twice.
- Lines 350-351: It must be highlighted that (Estimated) Breeding Values are dynamic values and should be updated in the database every time a new evaluation is performed. It is not like phenotypic value for a trait (e.g. size at birth) that doesn't change even if the individual grows up and is bigger at another age.
- Lines 357-360: I think that one of the main messages of the paper should be that different sources of information and different goals have to be included into the management criteria beyond the maintenance of global genetic diversity (minimisation of coancestry).
- Line 361: To be consistent with the part about the studbook and population management, some examples of QG software could be provided (for example programs to perform breeding values estimation).
- Lines 363-364: This sentence is incomplete.
- Line 367: It is not only the need of accuracy (e.g. pedigree completeness) but also to a standardisation of the way the measurements are taken between different facilities and across generations.
- Lines 372-373: This is the hard task. It would be nice to have a deeper consideration on the real applicability of these methodologies and to provide examples of cases where the situation is closer to this scenario and those where it would be nearly impossible.
- Lines 385-386: I think that the main task conducted in current exsitu conservation programs is the prioritisation of individuals to be reproduced based on their genetic relationship with the rest (before/besides the minimisation of the coancestry between pairs). This procedure acts jointly on the maintenance of genetic diversity and the minimisation of the rise of inbreeding.
- Line 402: I agree. It is clear that studies on insitu populations are needed to know the target traits and values to be pursued in captivity. And the same goals should be established for both environments.
- Line 404: It is difficult to deal with fitness itself. Sometimes it is more useful to concentrate on particular traits (main components of fitness).
- Line 405: There is an extra space before Bonnet.
- Line 409: Something missing between 'be' and 'to'.
- Line 418: I think that the first/main aim is to reduce the loss of diversity. Minimising inbreeding is a complementary aim, which should go together. Realise that it is hard to minimise inbreeding when little genetic diversity is present.
- Line 664: Capitalise Fisher and Wright.
- Line 696: Provide a caption to the Figure 2. Additionally, I think that the information presented in the left and right parts of the figure are different enough to deserve separated figures.
- Line 698: Is the word 'in' really needed between 'individuals' and 'might'?
- Line 700: Change the word 'or' by 'and' because in this scenario differences in environment.