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## Letter to the Editor

### 50/500 rules need upward revision to 100/1000 – Response to Franklin et al.

Here we refute Franklin et al. (2014) and clarify the basis of our recommendations (Frankham et al., 2014) on the 50/500 rules for effective population sizes ( $N_e$ ). These thresholds, required to avoid inbreeding depression in the short-term and loss of evolutionary potential in perpetuity (Franklin, 1980), need to be increased to 100 and 1000, respectively, along with corresponding doubling of the IUCN Red List Criterion C thresholds. Our responses to their main points are as follows:

First, Franklin et al. said that we had neglected natural selection (purging), but this is incorrect: we specifically reviewed the theory and empirical results (Appendices A4 and A5), and reached a different conclusion to them.

Second, they queried our revision of  $N_e = 50$ . Empirical data (post-1980) indicate that  $N_e = 50$  is insufficient to prevent inbreeding depression, and our revised recommendation of at least  $N_e = 100$  was based on a combination of theory and empirical evidence, as detailed in our review.

Third, they questioned the distinction between peripheral and fitness traits, but this difference is well-established in the quantitative genetics literature. In brief, peripheral (P) and fitness (F) traits differ on average in heritabilities ( $F < P$ ), inbreeding depression ( $F > P$ ), mutation reducing mean fitness ( $F > P$ ), extent of non-additive genetic variation ( $F > P$ ), in symmetry of selection responses ( $F > P$ ), as a consequence of being subjected to different types of natural selection (Table 2). The ability to adapt evolutionarily to environmental change depends on quantitative genetic variation for total fitness.

Fourth, they claim we "... have not presented new empirical results or convincing theory that justifies changing this guideline to larger values ..." We have addressed this for  $N_e = 50$  above. In relation to retaining evolutionary potential, we presented previously unpublished empirical data (Appendix Figures A1 and A2) that  $N_e = 500$  is insufficient to avoid loss of genetic variation for fitness, and used several lines of theoretical evidence to conclude

that  $N_e$  needs to be at least doubled. Further, post-1980 evidence revealed that  $N_e = 500$  might also be insufficient to maintain quantitative genetic variation for peripheral characters (Appendix A6).

Finally, as IUCN Red List population size thresholds under Criterion C derive from genetically effective population sizes (Appendix A3), and two of them explicitly from previous  $N_e$  of 50 and 500 thresholds, it is logical to update them too, by doubling the thresholds to reflect the revisions we recommend above.

While there remain uncertainties as to the required revisions of genetically effective population sizes for conservation, the arguments by Franklin et al. (2014) do not justify retention of the old 50/500 rules. In fact, our recommendations are conservative, as available evidence indicates that more than a doubling of  $N_e$  may be justified.

#### References

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