Response to Comment on “Individual heterozygosity predicts translocation success in threatened desert tortoises”

Peter A. Scott1*, Linda J. Allison2, Kimberleigh J. Field2, Roy C. Averill-Murray2, H. Bradley Shaffer3,4

1Department of Life, Earth, and Environmental Sciences, West Texas A&M University, Canyon, TX 79016, USA. 2US Fish and Wildlife Service, Desert Tortoise Recovery Office, Reno, NV 89502, USA. 3Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA. 4La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California, Los Angeles, CA 90095, USA.

*Corresponding author. Email: pete.a.scott@gmail.com

Hedrick brings up several potential concerns that he feels challenge or limit our main finding. Hedrick does not comment on our empirical results, but rather argues that several factors may confound or invalidate our conclusion. Many of these concerns focus on unknown ecological aspects of the translocated tortoises, but we believe there is no reason to conclude that they bias the results or interpretation as presented in our original paper.

Scott et al. (1) presented an analysis of the Large Scale Translocation Site (LSTS), one of the largest translocation studies ever conducted on an endangered species, and determined that individual heterozygosity, but not site of origin or distance moved, is an important predictor of post-translocation survival in desert tortoises. Hedrick (2) does not challenge this primary result, but rather our recommendation that heterozygosity may be a useful indicator of translocation success to improve conservation outcomes in this and other species. Scott et al. were transparent about the essential context of this long-term translocation program: Most tortoises died, many released tortoises were held in captivity before being released, and released tortoises had unknown histories. In addition, Hedrick criticizes our report for focusing on only a single fitness component, post-release survival. Hedrick argues that many of these unknowns compromise or invalidate Scott et al.’s conclusions. Here, we explain why these outstanding variables should not undermine our conclusions.

Although tortoises within the LSTS experienced very high mortality, there is little reason to assume that this mortality biased our results. As explained in (1), line transect surveys estimated that by 2015 roughly 2.1% of adult and juvenile translocated tortoises, or 4.2% of translocated adult tortoises, survived. Surveys of adult wild tortoises from the surrounding region also suggested a high annual adult mortality of ~9.2%. If that survival rate is compounded annually over the 19 years of the LSTS project, it translates to an overall survival of 16%. As pointed out in (1), and as Hedrick acknowledges, factors contributing to the lower survival in the LSTS may include crowding, compromised health, a high proportion (55%) of released juveniles, or the novel challenges imposed by translocation. However, the overarching point is that mortality, whatever the cause, is the very problem that thwarts translocation programs everywhere. Our data suggest that in this case, individuals with the greatest heterozygosity had higher survival over this critical period following translocation and release. There is no reason to suspect that this result is linked to the specific mortality schedule, be it high or low.

In a similar vein, Hedrick postulates that because we only sampled about 1% (87/9000) of the tortoises that perished, but 41% of the adults that survived, our sampling “suggests a much greater potential for nonrandomness, and therefore biased estimates of heterozygosity and survival, in the sample of dead tortoises.” Our 87 samples spread across space and time were matched to living individuals for sex and time of release, and otherwise were a random, unbiased sample of tortoises that died. There is no reason to suspect any bias with respect to heterozygosity.

Another concern raised by Hedrick is that many of the translocated tortoises spent some time in captivity, and that this again somehow led to the most heterozygous tortoises surviving after release. These tortoises may have been in backyards for decades or been found wandering a new subdivision and brought in by concerned residents; their individual histories are unknown and unknowable.
Countering Hedrick’s concern is published evidence showing that released captive tortoises, individuals translocated directly from the wild, and resident tortoises have roughly equal survival rates (3–5). In addition, there is no plausible reason why time in captivity should contribute to the differential survival of higher-heterozygosity individuals after translocation and release.

Hedrick suggests that translocation mortality might be caused by high levels of individual inbreeding (from captive breeding or other causes), rather than high heterozygosity indicating translocation survival. He provides a calculation of their relative inbreeding coefficient, using a standard model from neutral theory population genetics, $F = (H_{\text{exp}} - H_{\text{obs}})/H_{\text{exp}}$, and substituting the heterozygosity of survivors as a proxy for $H_{\text{exp}}$ and of those that perished as $H_{\text{obs}}$. However, the assumptions necessary for this calculation of inbreeding are not met in this system. We cannot assume that the mean observed heterozygosity of translocated tortoises is equal to the average heterozygosity of this species under Hardy-Weinberg equilibrium; individuals translocated to the LSTS were not drawn from a single panmictic population, and the heterozygosity estimate for survivors after translocation is not an appropriate proxy for $H_{\text{exp}}$, the population- or species-level expected heterozygosity. A more realistic approach for this calculation would be to use the proportion of dead and surviving tortoises translocated to the LSTS to calculate a weighted value of $H_{\text{exp}}$ based on the proportions of living and dead tortoises out of the total released. Doing so returns an inbreeding coefficient for dead translocated tortoises of $F = 0.0049$, which suggests that they are not inbred. More important, even if inbreeding rather than selection for heterozygosity is the mechanism behind our observation, we still would advocate for translocating the more heterozygous, and therefore more outbred, individuals.

Hedrick also takes issue with our use of inferred straight-line distance as a measure of translocation distance, suggesting that a more realistic migration path or habitat characteristic would be a better metric. We agree that realistic measures of distance, be they least-cost or ecological, would also be interesting to investigate. However, in this situation where the inferred origin of translocated tortoises had an error of ~36 km, neither the microhabitat nor the probable “tortoise migration distance” are estimable. Moreover, the standard use of straight-line distance is a reasonable measure of isolation-by-distance that is well established in this species (6, 7).

Hedrick raises many valid points, most of which were also raised in Scott et al. We wish we knew the proximate mechanism(s) driving the higher heterozygosity of surviving tortoises and could distinguish selection from inbreeding. It would have been ideal to have before-and-after baseline data to allow forward-in-time, rather than retrospective, analyses. It would be great to know the history of every tortoise, its pedigree, and its state of health at release, and be able to measure every fitness component of every tortoise. We absolutely agree with his final comment that genetic data should not be the only criterion, but one of many that are used in deciding which individuals to invest in for translocations. As we clearly state, “We are not suggesting that individual heterozygosity should be the only criterion for deciding which individuals to translocate: Local ecology, disease exposure history, and individual condition are some of the other factors that are often critical, and we stress the importance of verifying these results in other systems” (1).

REFERENCES

13 January 2021; accepted 23 March 2021 Published online 4 June 2021 10.1126/science.abg3199
Response to Comment on "Individual heterozygosity predicts translocation success in threatened desert tortoises"

Peter A. Scott, Linda J. Allison, Kimberleigh J. Field, Roy C. Averill-Murray and H. Bradley Shaffer

Science 372 (6546), eabg3199.
DOI: 10.1126/science.eabg3199