



# Reply to Hedrick et al.: Trophy hunting influences the distribution of trait values through demographic impacts

Coltman et al. (1) claimed that the “production of smaller-horned, lighter rams and fewer trophies” is “an evolutionary response to sport hunting of bighorn trophy rams.” Using data from the same population, we conclude (2) that the very rapid shift in body mass they report was principally demographic in origin rather than evolutionary. Our conclusions are further supported by additional research (3) that has demonstrated that the approach Coltman et al. (1) used to detect trends in breeding values gives unreliable results that are highly anticonservative.

Hedrick et al. (4) are correct in saying that we simulated body mass and not horn length. This was because horn data were insufficient to parameterize our model. Horn length and body mass are strongly correlated for Ram Mountain male bighorn (0.752). It consequently seems plausible our conclusions could hold for horn size also. Hedrick et al. (4), however, misrepresent our use of the inheritance function, which is different from heritability. The inheritance function is a regression of lamb mass at time  $t + 1$  on parental mass at time  $t$ . Contrary to Hedrick et al. (4), our approach captures maternal and paternal effects, as offspring mass is a function of both maternal and paternal mass.

Hedrick et al. (4) further propose that we conduct a standard quantitative genetic analysis using approaches that frequently fail to capture observed responses for wild populations (5). We requested data to conduct an appropriate analysis of trends in breeding values using methods in ref. 3, as it would have been straightforward to include information from such analyses in our model. We were told they were not available to us.

In the absence of these data, we chose to conduct a sensitivity analysis of model predictions to the male component of the inheritance function. We increased the estimate of paternal inheritance 10-fold. This did not substantially alter our conclusions that the very rapid decline in body mass and horn size that Coltman et al. (1) report is unlikely to be an evolutionary response. We are still prepared to conduct additional analyses if necessary data are made available.

We make all of these issues explicit in our paper and issue many caveats on the interpretation of results. We make no sweeping or irresponsible management recommendations. We very much regret the fact that D.W.C., M.F.-B., and F.P. withdrew their authorship: a distressing event that occurred once it became apparent that our model output contradicted their previous findings. We welcome constructive dialogue on our

paper but are disappointed by claims that misrepresent our analyses and demands that we use a statistical framework not available to us given that we did not have access to the necessary data.

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**1** Coltman DW, et al. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature* 426(6967):655–658.

**2** Traill LW, Schindler S, Coulson T (2014) Demography, not inheritance, drives phenotypic change in hunted bighorn sheep. *Proc Natl Acad Sci USA* 111(36):13223–13228.

**3** Hadfield JD, Wilson AJ, Garant D, Sheldon BC, Kruuk LE (2010) The misuse of BLUP in ecology and evolution. *Am Nat* 175(1):116–125.

**4** Hedrick PW, Coltman DW, Festa-Bianchet M, Pelletier F (2014) Not surprisingly, no inheritance of a trait results in no evolution. *Proc Natl Acad Sci USA* 111:E4810.

**5** Merilä J, Sheldon BC, Kruuk LE (2001) Explaining stasis: Microevolutionary studies in natural populations. *Genetica* 112-113(1):199–222.

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The authors declare no conflict of interest.

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