LETTER

Not surprisingly, no inheritance of a trait results in no evolution

Traill et al. (1) conclude that the "decline in body mass of the bighorn population is largely attributable to demographic change and environmental factors" and "expect our conclusions to hold for horn length too." Three of us (D.W.C., M.F.-B., and F.P.) provided data from the Ram Mountain bighorn sheep population for this article, but withdrew from authorship because of major concerns about the analysis and interpretations. The key problem we saw is an inheritance function that does not adequately model the inheritance of mass (and by implication inheritance of horn length).

The inheritance function is a regression of paternal mass on lamb mass, a measure similar to narrow sense heritability, with a slope of 0.0195 (figure 2*D* from ref. 1), which is not different from 0. This is not unexpected: lamb mass is primarily influenced by maternal effects and shows a very weak relationship with paternal mass and negligible additive genetic variance (2). A more appropriate approach would be to model adult paternal mass on the mass of similar-aged male progeny or to integrate previously published information on the heritability of mass and ontogeny of growth in this population (2–4). Adult mass in bighorns is significantly heritable, with an estimated narrow sense heritability of 0.32 (4), similar to that for body size in other species. Indeed, when Traill et al. assume a 10-fold increase in their inheritance function slope, they predicted a considerable decline in ram mass (figure 5 from ref. 1). This reduction was not unlike the first generation of the documented steady decline of both horn size and mass of adult rams of 25–30% observed over 30 y (about four generations) of harvesting (3).

Further, Traill et al. model hunting selection on body mass and not horn size. In trophy hunting of bighorn sheep, the hunter's primary goal is to obtain a ram with the largest horn size and not the largest mass. Given that the inheritance function was not for adult horn size and that they modeled hunting selection on adult mass, conclusions about the evolutionary effect of hunting on horn size are tenuous at best.

We agree that harvesting large rams influences the distribution of trait values through demographic impacts. To adequately model the relative importance of demography, environmental effects, and evolutionary response requires the integration of biologically accurate information. Traill et al. present a sophisticated and potentially powerful approach to predict changes in a trait in a hunted population; however, their analysis did not adequately incorporate the known inheritance of adult body mass in bighorn sheep. It is therefore inevitable that no evolutionary response was predicted by the model.

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1 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.

2 Wilson AJ, Kruuk LE, Coltman DW (2005) Ontogenetic patterns in heritable variation for body size: Using random regression models in a wild ungulate population. *Am Nat* 166(6):E177–E192.

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

4 Poissant J, Wilson AJ, Festa-Bianchet M, Hogg JT, Coltman DW (2008) Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep. *Proc Biol Sci* 275(1635): 623–628.

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