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[*Editor's note: The following "Letter to NATURE" was prepared and submitted to NATURE by Dr. Valerius Geist. It is in the format required by NATURE, and contains relevant lessons learned through trophy management for deer in Europe. NATURE chose not to publish this letter.*]

TROPHY MALES AS INDIVIDUALS OF LOW FITNESS (DRAFT)

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While wildlife trophies get a lot of attention in modern times in North America and Europe, such infatuation has a long and instructive history. Already in the Upper Paleolithic, cave painters invariably chose to paint large, complex antlers on male deer and long horns in ibex, bison, and wooly rhinos [1]. The trophy mania hit its high point in medieval central Europe when huge red deer antlers were used as gifts of state, when

hunting records of nobility were recorded in exquisite detail and antlers were venerated objects of display in castles built to house trophy collections[2]. Such castles have survived into modern times, i.e. the castle of Moritzburg close to Dresden, Germany displays red deer of unequalled size[3]. These have, naturally, raised the question, "How might such antler growth be duplicated?" Moreover, in the late 19th and early 20th centuries, the vagaries of treatment of wildlife in central Europe led to declines in the trophy quality of antlers which lead to an early "Quality Deer Management" movement[4]. This movement reversed the decline within about a quarter century, and generated an intense interest in how to produce huge trophy antlers. We see, currently, in the United States the birth of a similar "Quality Deer Management" movement[5,6]. Some of the most interesting experimental deer management for trophies was carried out during the Third Reich on the Rominten Heath by Walther Frevert[7]. There is, consequently, a rich historical background on the biology of "trophy males," but this is currently poorly known.

The recent study by Coltman et al.[8] which demonstrated declines in horn and body size in bighorn rams with hunter selection for large-horned males, confirms the findings from the late 19th and early 20th centuries on European cervids[9,10,11]. The ongoing removal of males with superior antlers led to a severe shift in sex ratio in favor of females. This imbalance was primarily addressed by the culling males with inferior antlers, while sparing males with good antler growth. Wildlife eugenics, the culling of undesirables, was made popular by Ferdinand von Raesfeld's "Hege mit der Buchse"[12] (husbanding with the rifle) which subsequently was institutionalized in Germany's 1934 wildlife management legislation[13]. One thus suspects that, contrary to Coltman et al.'s fears, the declines in horn and body size in bighorn rams are not permanent, but can be reversed by similar means. Even if merely left to themselves, the selection pressures favoring horn size in bighorns[14] would return normal horn growth in time. Moreover, the rehabilitation of formerly strip-mined bighorn habitat in Alberta[15], as well as the reintroduction of bighorns to former ranges throughout the United States has not merely increased the wild sheep population of the continent by nearly 50 percent in a quarter century[16], but has also resulted in the growth of many rams with record-sized horns[17].

In central Europe, management for trophy deer also led to deliberate population reductions, habitat improvements, and the introduction of males with superior antlers from other regions[18]. The latter, however, was considered a failure[19]. The interest in improving trophy quality led to research into the nature of body and antler size variations in red deer, with the aim of reproducing antler sizes such has been seen in medieval times [20,21,22,23,24]. This illuminated the "biology" of trophy males in clinical detail and led to surprises. One can summarize the findings as follows: Deer varied in body size along a peadomorph-hypermorph axis, so that small-bodied deer retained juvenile proportions compared to large-bodied deer[25,26]. Body size was plastic, but slow to shift and it took some five generations for medium-sized deer to reach maximum body size[27]. This finding, rediscovered three decades later, was labeled the "maternal effect'[28,29,30]. Continuous access to highly digestible feed rich in protein calcium, and phosphate was a necessary condition for large antler and body size. However, trophy stags were exquisitely sensitive to shortages in food quality[31], which indicates that medieval foresters must have been very concerned about the possibilities that their treasured and

pampered stags might move off somewhere else. It explains, in part, the brutality with which these foresters treated peasants who disturbed deer. While a high plane of nutrition was a necessary condition for exceptional antler growth, it was not a sufficient condition in itself. Optimal results were achieved by artificially preventing males from rutting[33]. Males that did not rut had no need to heal the severe rutting wounds suffered by rutting males[33], and were thus able to shift their body resources from repair and re-growth into increased body and antler growth. Moreover, the absence of wounding would lead to the desirable symmetrical antler growth.

However, stags that reached maximum antler development were severely handicapped by their unwieldy antlers in fighting and tended to lose out to normally-antlered males. Not infrequently trophy stags locked their complex antlers and died[34]. Large trophy antlers conveyed no apparent benefit to their bearers, quite the contrary. This suggests that in free-living populations, male deer with exceptionally large antlers may be non-breeders, and thus individuals of low fitness[35]. During eight years of field work with habituated mule deer in Waterton National Park, Alberta, Canada, I was fortunate to closely observe three bucks with exceptionally large antlers. All three became "shirkers" during the rutting season. They avoided other deer, bucks especially, and thus failed court and breed females. They merely fed and rested in seclusion. However, one of these bucks had a surprising history. He had been a normal rutting buck up to three years of age. During a fight with an old buck, he was flung upward and landed on his back in some wind-blown aspen trees. He quit rutting that year and for two more years. By then, he had grown to a very large body and antler size. The next rutting season he reversed and became a fully engaged, breeding master-buck. He continued as such for three rutting seasons. Hence, "shirking" is potentially reversible. Nevertheless, managing populations for trophy size remains highly questionable, as do the stated concerns of Coltman *et al*.

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[Editor's Note: Ray Lee and I also prepared a letter of rebuttal to NATURE. We focused on Coltman et al.'s allegation that insufficient attention has been given to protection of male social structure by modern managers and the political nature of wildlife management in the USA. When we learned Dr. Geist's letter had been rejected, we didn't bother to submit ours. It was too long anyway. I've left it in the draft NATURE format. WEH]

UNDESIRABLE CONSEQUENCES OF UNQUALIFIED SPECULATION ON THE NEGATIVE EFFECTS OF TROPHY RAM HUNTING

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