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Special communication

Defining subspecies, invalid taxonomic tools, and the fate of the woodland caribou

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My concern pertains to the true woodland caribou, the uniformly dark, small-manned type with the frontally emphasized, flat-beamed antlers. Judging from the low complexity of its nuptial characteristics, it is probably the oldest and most primitive *Rangifer* alive. Whether the taxonomic name *Rangifer tarandus caribou* Gmelin 1788 is applicable to this form is uncertain as the type locality given is Quebec City and a true geographic location for the type specimen is thus lacking. The true woodland caribou is scattered thinly along the southern rim of North American caribou distribution. It needs urgent attention, but the urgency is compromised by a flawed taxonomy. This flawed taxonomy, using - in this case misusing - the authority of science, suggests that there are far more "woodland caribou" than there really are. A re-examination of caribou subspecies is urgently required.

Frank Banfield (1961) made the subspecies *Rangifer tarandus caribou* Gmelin 1788 a catchall for larger caribou. He lumped into this subspecies not only the (a) true woodland caribou, but also (b) the totally different Newfoundland caribou (*R. t. terreanovae* Bangs 1896), the (c) form closest related to true woodland caribou, but nevertheless biologically distinct barren-ground form, the Labrador caribou (*R. t. caboti* Allen 1914), as well as the (d) totally different western Osborn's caribou (*R. t. osborni* Allen 1902) from British Columbia. The latter is so different from the dark woodland form (called the Mountain caribou in British Columbia and found to the south of the Osborn's

caribou's distribution) that even bush pilots I flew with noted the difference, let alone a competent taxonomist such as Dr. Ian McTaggart-Cowan who segregated the two forms in his and Charlie Guiguet's (1965) *Mammals of British Columbia*. All of the above forms can be identified or differentiated visually at a glance by differences in the mature bull's coat and antler characteristics. Even cave artists from the Upper Paleolithic sketched the coat and antler characteristics of European tundra reindeer correctly. That's how distinct nuptial characteristics are!

In addition there is talk of "mountain" and "woodland caribou" north of 60. However, we appear to be dealing here with splinter populations of barren ground caribou, which have adapted to a more sessile life style, increased in body size and assumed some "woodland mannerisms". This needs close scrutiny and clarification!

Consequently, on the face of it we have "woodland caribou" roaming Canada from Newfoundland and Labrador right through British Columbia and well into the Yukon Territory, North West Territories, and Nunavut. And that is an artifact of a taxonomy based on an inappropriate methodology. Therefore, the populations unjustly labeled woodland caribou or subspecies *caribou* obscure the fact that the true woodland caribou is very rare, in very great difficulties and requires the most urgent of attention.

Banfield did spend time with barren ground caribou, but I do not know if he even saw Labrador or

Newfoundland caribou, let alone the difficult to reach western Osborn caribou (which I observed frequently during 1961-65 on my Stone's sheep study area in the Spazisi, about 130 km south of Telegraph Creek, BC). Secondly, he may not have had an "eye" for details in a picture-plane. I am aware of this difficulty in individuals with minimal artistic talent or training, because, having sketched different subspecies of big game for court or publication purposes, I have asked colleagues how the sketches differed. Some said that, yes, they do look different, but they could not detail why they were different. To such a person, all caribou might look much the same. Nevertheless, even in 1961 when Banfield's monograph came out, my then mentor Ian McTaggart Cowan, who wrote two major taxonomic monographs (on mule and black-tailed deer [*Odocoileus hemionus* Rafinesque 1817] and American sheep [*Ovis dalli* Nelson 1884, *O. canadensis* Shaw 1804]) considered that monograph unacceptable! So, my concerns with Banfield's inadequacies in his taxonomy of caribou are not new.

Banfield (1961) fell victim to an error, which is, unfortunately, not uncommon in taxonomy: he used comparative morphometrics to distinguish subspecies. That is, while descriptions of color, hair and antler patterns appear to be "subjective", skull measurements appear to be "hard" and amenable to "objective" analysis. A statistical analysis of measurements appears to be "scientific". Unfortunately, that assumption is false! A comparison of skull measurements between populations, no matter how voluminous the data set or how refined and sophisticated the statistical tools, cannot be used taxonomically, because such an analysis confounds and confuses genetic variance, epistatic variance, the compounded, multiple environmental variances as well as true statistical variance. And there is no way to disentangle and pronounce on such.

Comparative morphometrics cannot - in principle - be used in taxonomy. However, because of its great precision it can be used forensically, or it can be used to illustrate growth trends, etc. It's a fine tool, but not to identify *genetic* differences. It cannot do that on principle. Unfortunately, this fundamental error has been done frequently in the taxonomy of various mammals (Geist, 1991, a; b; c). Moreover, taxonomy is now contained in legislation and subject to court action. Having been cross-examined in one case for six days for some 24 hours on red deer taxonomy, I speak from experience (Geist, 1992). Because of far-reaching legal consequences, it is vital to clarify terminology and concepts used in taxonomy (Cronin, 2006), distance oneself from flawed methodology, and seek robust, workable criteria for classification.

Consequently, let me please elaborate a little about morphometrics. As skulls are plastic in their growth,

the same genetic system - depending on nutrition and stresses during ontogeny - can generate infinite varieties of skull forms and sizes. In addition, skull size and shape are linked by allometry. Size and proportions are, therefore, linked, and differences in proportions have nothing to do with differences in genetics. Nor do differences in size, which are primarily driven by net-nutrition. Within a subspecies, such as the Central European red deer (*Cervus elaphus hippelaphus* Kerr 1792), body size due to differences in habitat quality can differ five fold (from 70 kg adult stags from very poor industrial habitats to 350 kg stags from the Carpathian mountains). These types of growth differences have been long explored experimentally by the agricultural discipline of Animal Science, and they are nothing new. Also, nutrition experiments have been done that more than doubled "normal" body size of red deer within five generations. This splendid work by Franz Vogt is virtually unknown as it was published in German (Vogt, 1936; 1946; 1951). Nor is the taxonomic thinking based on such known here for the same reason (I have integrated such, among others, in my 1998 book *Deer of the World*. See references there).

It is not fair to single out Banfield for criticism. Others also committed the far-reaching error, namely, to apply straightforward comparative morphometrics to taxonomy (i.e in bison or sheep see Geist 1991b; 1991c). Only under rare circumstances can one draw on comparative morphometrics to argue for probable, but unproven, genetic differences and neither Banfield nor zoologists in general are aware of these. One of the first taxonomists to pioneer comparative morphometrics was the Norwegian Ingebrigtsen (1923) who used such to demonstrated paedomorphism in red deer. Ironically, that happens to be a correct use of that methodology! I hunted down Ingebrigtsen's 1923 monograph in Memorial University in the 1970s - and had to use a razor to cut open the pages. It had never been read in all its 50 year of existence in North America!

That gets us back to square one: what is a subspecies? Mayr (1963) defined a subspecies as an aggregate of populations in a geographic subdivision of the species' range that differs taxonomically from other populations. If one can distinguish the individuals from different populations by *taxonomically valid criteria*, then each population so distinguished is a subspecies. The populations may differ greatly by *taxonomically invalid criteria*, in which case they are not subspecies, but *ecotypes*. This applies, for instance, to populations of the phylogenetically most advanced of the elk (*Cervus canadensis canadensis* Erxleben 1777). All elk in North America have exactly the same coat pattern, antler characteristics and rutting

voice as well as the same genetics (see Geist, 1998). The one gene difference between Olympic elk and Rocky Mountain elk is taxonomically trivial. That's why there is only *one* subspecies of elk in North America and the regional differences, primarily in body size and environmentally affected growth-patterns of the antlers are *ecotypic*. Moreover, elk with exactly the same *nuptial* characteristics as North American elk are found in Mongolia and Siberia. Ergo, the subspecies *C. c. canadensis* Erxleben 1777 inhabits two continents. Genetic studies have born this out (Ludt *et al.*, 2004).

One possible way to characterize subspecies is to segregate populations by their nuptial or rutting dress, or "uniform". These characteristics vary with the age of the males, are minimally affected by environment and are best expressed in old males at breeding time. Biologically, this suggests that selection for nuptial characteristics is done through female sexual selection. Genetic studies on deer, in which specimen were selected rigorously by nuptial characteristics, generated very clean segregations (Ludt *et al.*, 2004), suggesting minimal gene flow between subspecies. This matches field observations, as subspecies of the "red deer" complex appear to differ ecologically, while narrow or missing hybrid zones speak of hybrid disadvantage. Such subspecies are thus biologically real. The non-abstract reality of the subspecies makes it, ironically, the old *Linnean species*. Social adaptations thus reflect common descent and segregated gene pools, and are thus useful characters for taxonomy. Note: using the criterion, nuptial characteristics, drastically reduces the number of subspecies as listed; for instance, in O'Gara (2002), because it eliminates the confusion of subspecies and ecotypes.

Subspecies cluster naturally into species, whose unifying feature is an identical *adaptive syndrome*. Again, please let me illustrate with the latest in "red deer": the cluster of wapiti/maral deer are six-pronged *cursors* (runners), the Himalayan cluster are 5-pronged *saltors* (jumpers). These two clusters represent two different adaptive syndromes, and, therefore, two different *species* of "red deer" as they differ entirely in their anti-predator adaptations and require very different landforms (level, open sub-alpine/sub-arctic steppe versus steep, long, shrub-covered mountain slopes). While both are close in mtDNA, they are in morphology farther apart, than either is from the more distantly related third species, the European red deer (saltatorial/cursorial body form). Genetic data reveals here three long-segregated genetic clusters (Ludt *et al.* 2004), morphology indicates greatly different adaptations, and field observations confirm clean segregation. Here the *criterion* for the taxonomic *species* classification is *adaptation*, while the genetic data (phylogenetic lineages) is in a support

position, confirming a long-standing genetic segregation. Consequently, there are three species of "red deer". In zoos one can interbreed deer across genera, making *potential interbreeding in captivity* an irrelevant taxonomic consideration. The *Biological Species* of Ernst Mayr, falls out as a necessary consequence of evolving different adaptive syndromes and is applicable only to animals living under natural conditions that include predation.

The nuptial dress criterion works well with the subspecies of red deer and mule deer. And I - tentatively - think it works with *Rangifer* as well. Consequently, I applied it in my 1998 *Deer of the World* (pp. 324-328). However, it was presented there as a challenge. I suspect that it will work with caribou, but I would sleep easier if it could be based not on a few dozen, but on thousands, of individuals compared.

I emphasized the above because the subspecies criterion - *nuptial characteristics* - does not apply to white-tailed deer (or cougars, grizzly & black bears, wolves, etc.). For white-tails, we need to draw up separate subspecies criteria, though I do not currently know which. White-tails show huge regional genetic differences that do not reflect themselves either in their minimal external differences nor in the taxonomy based on skull morphometrics. White-tails from South America differ genetically more from white-tails in Georgia, than do Georgian white-tails from California coastal black-tails. The genetic differences within a species are here greater than between species (see Geist, 1998).

I was excited by Matt Cronin's *et al.* (2005) caribou paper. It basically fits the *Rangifer* taxonomy I suggested. However, it is necessary to study thoroughly the nuptial coat and antlers in *Rangifer* to see if integration between purported subspecies as I defined them does or does not exist. The Newfoundland caribou is by nuptial characteristics a subspecies. I think that true woodland and Labrador caribou segregate cleanly as their differences relate to radically different breeding biology. I think that the southern caribou in BC, the mountain caribou, has the same pelage and antler characteristic as the true (or very dark) woodland caribou and thus may be the same subspecies. Osborn's caribou are quite different from true woodland or BC mountain caribou, a conclusion supported also by Cowan and Guiguet in *Mammals of British Columbia*. I think the mountain caribou of the Yukon and NWT are non-migratory barren ground caribou.

Clearly, we need a thorough review of caribou taxonomy.

In short, if my argument is valid, then true woodland caribou are only the very few, dark, small-manned caribou scattered across the south of caribou distribution. They need the most urgent of attention.

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