Endangered species and the law

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Taxonomy does not deserve its reputation as an arcane science. As the following examples from ungulate taxonomy show, classification has important implications for conservation legislation.

THE science of taxonomy may be thought of by many as an arcane subject, innocent of the problems of the real world. But when taxa became included in conservation laws, this innocence vanished. Endangered species acts, wildlife management laws and the Convention on International Trade in Endangered Species (CITES), essential, if imperfect, tools for conservation, label species and subspecies with formal taxonomic names. Such taxa, elevated to legal status, became subject to legal action. That may place biologists, accustomed to privacy, anonymous peer review and uncertainty in knowledge, in the witness stand, subject to hostile cross-examination. In one Canadian court case I was questioned for 24 hours on the taxonomy of red deer (Cervus elaphus Linnaeus, 1758). The case led to fines of \$25,000 for the defendant, who argued that by crossing two (invalid) subspecies listed in legislation he had created a new form of life, and that laws controlling commerce in wildlife did not apply to his creations.

Implications

It is not the image of scientists squirming in witness chairs that merits attention, rather the fact that courts and solicitors' offices are allowed to rule on taxonomy. Judges may now decide on matters such as the definition of species or subspecies, the criteria for establishing taxa, which taxa are valid, and which populations can be legally protected. The implications for conservation, but also for biology in general, are profound and worrying.

Collectors, scientific or otherwise, are playing risky games taking chances on taxonomic uncertainties, for taxonomic mislabelling may now be a breach of law. That is no trivial matter if it leads to stiff fines or imprisonment, in particular if it brands the perpetrator a criminal. Even without such draconian consequences, the repercussions may be serious enough, as shown by the "Chinese argali" case (Fig. 1). Argalis (Ovis ammon Linnaeus, 1766) are giant sheep from central Asia, one of which, the Tibetan argali (O. a. hodgsoni Blyth, 1840), is on the endangered list of the US Endangered Species Act. Four Argali rams, shot in April 1988 by four US hunters in Ganzu Province, China for a payment of \$100,000, were confiscated by agents of the US Fish and Wildlife Service upon entry to San Francisco. The hunters had been accompanied by an employee of the service, who was on temporary loan to the Smithsonian Institution. The trophies were labelled merely as O. ammon on the export permit. The sheep were subsequently identified as Tibetan argalis by four experts, but this was disputed by the hunters.

Although the case was eventually settled out of court, it had wide repercussions. It led to hundreds of thousands of dollars in attorney fees, a Grand Jury investigation, a flurry of diplomatic activity between the United States and China, embarrassing publicity, serious rifts within the US Fish and Wildlife Service and within the International Union for the Conservation of Nature over policy, several international meetings on caprid conservation and formal taxonomic and status reviews. The case embroiled two secretaries of the interior, five senators, two congressmen, affected even Secretary of State James Baker, and led to frantic activity to 'de-fang' the Endangered Species Act by some hunters' organizations. Pressure was exerted on scientists acting as expert witnesses to change their testimony, and they were maligned or blackmailed. Nearly four years afterwards, the affair is not yet over.

Species identity

The use of alloenzymes and mitochondrial DNA analysis has thrown doubt on the identity of some species named in conservation legislation. Eastern timber wolves (Canis lupus Linnaeus, 1785) and wolves (*Canis lupus* Linnaeus, 1785) and the red wolf (*C. rufus* Audubon and Bachman, 1851) may carry the mitochondrial DNA of coyotes (*C. lat-rans* Say, 1823)^{1,2}, whereas Florida panthers (*Felis concolor coryi* Bangs, 1896) carry genes of pumas from central America because of a release of hybrids decades ago. These cases have generated concern since the US Solicitor's office of the Department of the Interior ruled that hybrids are not protected by the Endangered Species Act³⁻⁵. Although I agree with O'Brien and Mayr³ that the hybrid policy should be carefully applied on a case-by-case basis, and that hybridization need not be a tragedy for conservation, the unresolved question is whether the courts, rather than other

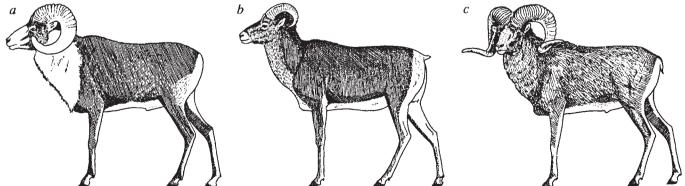


FIG 1 *a*, Mature Tibetan argali male (*Ovis ammon hodgsoni* Blyth, 1840) in nuptial pelage. There are at least 15 synonyms for this subspecies. *b*, Juvenile Tibetan argali male described as *O. a. dalai-lamae* Przewalski, 1888. The type specimen had the diagnostic dorsal neck ruff removed in mounting. It was later replaced with an altered mount of a mature *hodgsoni* male from another mountain range whose large horns had been removed and replaced with small horns. *c*, Mature Shansi argali (*O. a. jubata* Peters, 1876), negligently lumped with *O. a. darwini* Przewalski, 1884, due to a failure to read (but not to reference and denigrate) Peters' impeccable scholarship. The designation *jubata* has been applied to the *hodgsoni* specimen shot in 1988 in the Ganzu Province of China.

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specialists, will concur with their view. Moreover, to succeed in court, there needs to be agreement on the criteria to use when applying the 'hybrid policy'. As I discuss below, one such criterion should be the success of hybrids as tested in their natural habitat.

Taxonomic flaws may have severe consequences for conservation, and Canada's 'wood bison' (Bison bison "athabascae" Rhoads, 1897) are a case in point (Fig. 2). These bison are enshrined as a formal subspecies in legislation, and have been subject to a longstanding. well-publicized national conservation effort. Recently, a consortium of agencies led by Agriculture Canada (including the interagency organization in charge of 'wood bison' conservation), proposed that the bison of Wood Buffalo National Park, as carriers of bovine brucellosis and tuberculosis, be eliminated and replaced with disease-free 'wood bison'. A federal review panel agreed with the consortium.

The proposal sparked controversy even beyond Canada's borders. The park bison are derived from about 1,500 native bison and 6,673 (diseased) southern-plains bison moved to the park in 1925. The 'wood bison' are captive offsprings from bison captured in the northern part of the park that were once thought to have escaped hybridization. If 'wood' and 'plains' bison are valid subspecies, then the park bison are hybrids and, as such, the consortium argues, are not worthy of conservation. Not only was the taxon athabascae based on an inadequate second-hand description of a single specimen and subsequently on worthless taxonomic methods, but when the animals were properly fed, the characteristic hair coat of 'wood bison' transforms into that of 'plains bison' within about a year.

Wood bison are, consequently, not a taxon, but an ecotype (and an artefact of captivity at that⁶). Genetic analysis shows that 'wood bison' herds differ no more from plains bison herds than one from another. The designation of 'hybrid' for the park bison is thus false on taxonomic and genetic grounds. The species B. bison Linnaeus, 1758 has no subspecies, and that turns official conservation policy on its head. The park bison, still under selection pressure from predators, are not the worthless hybrids defined by officialdom, but are the most diverse, naturally tested gene pool remaining of the species B. bison. Replacing them with an inbred 'wood bison' ecotype, untested for decades by predators, would not only confuse phenotype with genotype, but would undermine the essence of conservation.

Clearly, taxonomy is important in a tangible sense. Yet worthless taxonomic methods, ignorance about the biology of NATURE \cdot VOL 357 \cdot 28 MAY 1992

taxonomic criteria, failure to review original and foreign-language literature, faulty curation, tampering with museum specimens and labels, and artistic licence in illustrating taxa not only cast doubt on standards of scholarship in taxonomy⁷, but reduce the effectiveness of science in providing urgently needed legal protection to various forms of life. Already the American Society of Zoological Parks and Aquaria has expressed doubt about formal taxonomy, and is focusing instead on "genetically significant" populations as subjects of conservation. But this is no substitute, in my view, for an improved, formal taxonomy.

A fatal flaw in much large-mammal taxonomy is the use of comparative morphometrics as a taxonomic tool. Comparative morphometrics of crania or skeletons of free-living populations can no more be used to measure taxonomic (genetic) differences than a rubber band can be used to measure distance. Every set of comparable measurements conceals genetic, epistatic, environmental and statistical variation. That is, the gross variation is a mixture of different types of variation, within which the genetic variance is undefined. It remains indefinable, despite various approximations. Comparative morphometrics as a taxonomic tool is logically flawed. It confuses phenotype with genotype, analogy with homology, ecotype with taxon, and does not reveal the taxonomic and evolutionary differences between the populations compared. It reveals only differences, the origins of which remain obscure.

This flaw is not uncommon in other fields of biology⁸ when quantitative comparisons between populations are used to bolster evolutionary analysis. Such comparisons are futile if the proportion of variance attributable to heredity is unknowable. The closer the relationship between populations of a given form, the more speculative must be the conclusions about evolutionary relationships, because large phenotypic differences can arise from closely related genotypes in different environments. Taxonomic or evolutionary differences in close relatives should be studied experimentally, provided different variables affecting ontogeny are subject to effective control.

Taxa determination

In the absence of quantitative factors that are firmly (experimentally) based on genetic expression, what criteria might one use for determining taxa at the species and subspecies levels? The 'biological species concept' defines the species level in sexually reproducing organisms by using incompatibility of reproduction as an objective distinguishing criterion. Undoubtedly, this is a good and sufficient criterion in many

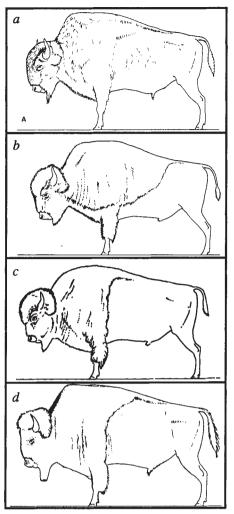


Fig 2 *a*, Classical 'wood bison' phenotype, Elk Island National Park. *b*, Bull from the same bison herd as *a*, but held and fed in a paddock in Banff National Park. *c*, Classical 'plains bison' phenotype. *d*, Wood bison bull from the same origin as *a*, but living free in the Mackenzie Bison Sanctuary. (From ref. 6.)

cases, particularly in species-rich communities with much sympatry. But this criterion, narrowly interpreted as the absence of hybridization in captivity by some⁹, is biologically flawed. This is painfully evident in the case of ruminants in the palaearctic and nearctic biogeographical domains, as widely differing forms hybridize readily in captivity, and the hybrids grow into adults under human care. But survival into adulthood is unlikely in natural conditions, where the hybrids are frequently exposed to predation. For instance, we found that hybrids of white-tailed (Odocoileus virginianus Boddaert, 1785) and mule deer (O. hemionus Rafinesque, 1817), which may develop in captivity into truly magnificent specimens, suffer from severe deficiencies when it comes to tactics and strategies of predator avoidance. The parent species have quite different means of escaping predators,

whereas hybrids have non-functioning mixtures of parental escape behaviours, plus inefficient locomotion. Escape strategies and tactics are, evidently, under close genetic control.

Is the current attempt to classify sika (Cervus nippon Temminck, 1837) and red deer into hybrid populations in several European localities^{10,11} an artefact of the absence of predators? In Manchuria, where both forms are sympatric, the populations remain distinct despite an occasional hybrid. Reproductive compatibility does not necessarily define a species, and sika and red deer differ in anti-predator strategies. Applying the conventional biological species concept would include in the same species hybrids that are not viable in nature. Viability of between-population hybrids under natural conditions of predation appears to be a better criterion for 'species'. It is a severe test, for even hybrids between subspecies may show loss of viability. This is suggested, for instance, by narrow hybrid zones, by ecological separation between some subspecies of Asiatic red deer, and by some difficulties in the hybridization of European red deer and North American wapiti.

Taxonomy without an understanding of ecology may have little relevance. Yet obtaining such understanding is difficult or even impossible today because of the widespread destruction of natural environments and the concomitant holding of large mammals in small populations in predator-free, artificial environments. The criterion of viability in natural environments will become increasingly difficult to test in the field, though experimental exposure of hybrids to predators, for instance, may be helpful. Consequently, species could be defined heuristically, as the next level of dissimilarity above the subspecies level, a practice adopted by those studying caprid biology¹²

Although O'Brien and Mayr³ defined subspecies geographically, this should be a fall-back criterion at best, as geographical origin has to be accepted on faith. For conservation laws to function effectively, one needs to be able to establish the geographical original of specimens by factors intrinsic to the specimen. How could one spot that a protected species or subspecies was being imported without recourse to the label stating its origin?

The nuptial hair coat of reproductively active adults is an old, widely used taxonomic criterion for subspecies, but only in some lineages. Circumstantial evidence suggests that nuptial hair patterns are under close genetic control in almost all cases. Bison appear to be unique among large mammals, as the structure of their hair coat varies en-

vironmentally, just as do antlers in deer. The nuptial coat of adult mammals as a taxonomic criterion delineating subspecies can be applied accurately only with an understanding of sex, age and seasonal differences, as well as some knowledge of the effects of transplants to different environments.

Uniting populations with the same nuptial 'uniform' into one subspecies greatly reduces splintering of species based on meaningless morphometric differences. But it may obscure real genetic differences in ecological adaptations between populations which deserve to be recognized formally. This is difficult to accomplish, with few exceptions. One such exception is the bighorn sheep (Ovis canadensis Shaw, 1803) of North America. Although the 'uniform' is nearly the same in all sheep of this species, there are differences based on ecology, such as the short hair-coat. large ears and long tooth rows of sheep adapted to hot deserts. Some species, however, such as bears, cougar or whitetailed deer, are amenable neither to subspecific distinctions by nuptial dress, as they look much the same no matter where they live, nor to differences in morphology based on differences in ecological adaptations.

White-tailed deer, an ancient and very successful species, have a distribution from just short of the Arctic Circle in Canada, to 18° south of the Equator in Peru. Although they differ in such social features as presence or size of the metatarsal gland, or the relative size of the tail, or in ecological adaptations such as differences in the shedding patterns of the seasonal hair coats, these differences are overshadowed by the great uniformity in nuptial dress. Differences in size and antler morphology are not taxonomically meaningful, because these features vary greatly with environmental quality and seasonal factors. Yet, although remarkably uniform in external appearance, white-tailed deer in South America differ more genetically from white-tailed deer in North America than do white-tailed deer from black-tailed deer in North America. White-tails also differ genetically between regions, without these differences reflecting conventional 'taxonomic' differences^{13,14}. A white-tailed deer's geographical origin cannot be determined from its morphology, as can be done with reasonable accuracy for black-tailed deer, wild sheep, ibex or even red deer.

Species definition

How then does one define useful taxonomic units within such a species? Should one define subspecies genetically? That may be necessary, but it has pitfalls, as the Canadian bison controversy reveals. Genetic analysis shows that different

plains bison populations differ somewhat and are, roughly, equidistant from one another. All plains bison arose at the turn of the century from the same stock based on about 90 bison captured between 1873 and 1886. The differences between herds appear to be meaningless captivity effects, generated in part by the founder effect and subsequent drift in small herds. A further reduction in genetic diversity should arise in tiny founder herds when the dominant bull displaces others from breeding and, after breeding several cohorts of daughters, is displaced in turn by his larger sons. His sons go on to breed from their mother, aunts, sisters, daughters, cousins and so on. The male-dominance effect in small founder herds thus promises to narrow and distort genetic differences.

Should differences that arise from random factors and captivity effects be part of taxonomic nomenclature? One could generate 'subspecies' ad infinitum with every founding herd. We assume that the genetic differences between taxa are linked to adaptions to natural environments, otherwise taxonomy does not reflect the natural order of life. We must be careful to ensure that this order is not drowned out by the 'genetic noise' of man-made artefacts.

Clearly, the taxonomy of large mammals needs to be rethought. Taxonomy has gained greatly in importance since the advent of conservation legislation, and must be freed from neglect by proper funding and by intelligent practitioners. The dismantling of museum collections is not only tragic, but irresponsible, now that the specimens have gained legal significance. Without good collections and good taxonomists, signatories to international conservation conventions cannot adequately manage conservation within their own borders, let alone live up to their international obligations. \Box

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