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Poor taxonomy and genetic rescue are possible co-agents of silent extinction and biogeographic homogenization among ungulate mammals

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SUMMARY

Genetic rescue is a measure to mitigate the effects of reduced genetic variation in endangered small, isolated (inbred) populations by introducing new genetic variation into such populations. This is usually accomplished by translocating individuals from a related population, assumed to belong to the same, often polytypic species, into the endangered population. If, however, the taxonomic classification does not reflect the ‘true’ diversity, genetic rescue can have detrimental effects on the survival of the endangered population (e.g. outbreeding depression). Here we point to problems if erroneous taxonomy informs such translocating strategies. Actions that promote artificial admixture of evolutionary lineages may be ineffective, or they may homogenize existing diversity and biogeographic patterns instead of protecting them. The extreme result is to drive target species and/or cryptic lineages to silent extinction. We single out conspicuous examples to illustrate the negative impacts of actions, which have resulted from artificial interbreeding of evolutionary distinct species or ill-conceived ‘genetic augmentation’. In such cases, translocations negate the overarching objective of biodiversity conservation: embodied in

the concept of phylogenetic distinctiveness (PD), the encompassing scientific foundation of biodiversity conservation aims to maximize representation of the evolutionary history at the levels of species and ecosystems. A major underlying problem that we identify is persisting taxonomic inertia maintaining e.g., an overly simplified ungulate taxonomy, which is in most cases equivalent to a certain genomic incompatibility or a dilution of specific adaptations. Translocations and genetic rescue should only be employed, if potentially negative effects of the measures can be ruled out (including wrong taxonomy). Poor taxonomy has been – and indeed remains – at fault.

INTRODUCTION

Here we examine how the taxonomic treatment of threatened species influences outcomes of conservation interventions. We examine, in particular, the implications and impacts of errors in classifications of populations that are targets of genetic rescue (advocated as a prominent action in conservation). Genetic rescue aims to restore gene flow to small inbred populations of outbreeding organisms that have become isolated by human activities within the past few centuries (cf Frankham et al. 2015, Ralls et al. 2018). We focus on endangered ungulates particularly, because many species include prominent examples of conservation concern, and these large mammals are also actively managed by game ranchers.

Moreover, the ungulates exemplify how taxonomy has become an increasingly neglected arena of scientific research through the 20th century (Wheeler 2008, Cotterill 2016). Too often, overly simplified classifications of these vertebrates were (and are still) accepted uncritically, and taxonomic revisions of large mammals reliant on representative sampling and modern methods are the exception. The classifications of large mammals, primates and ungulates especially, illustrate a persistent ‘taxonomic inertia’ (Groves and Grubb 2011, Rylands and Mittermeier 2014, Gippoliti et al. 2018). Although the negative impacts of an overly simplified taxonomy are rarely recognized, let alone questioned, one early exception was the biologist Oscar de Beaux. He recognized the undesirable impacts of a simplified taxonomic treatment of biotic diversity at the species level on scientific knowledge – on biodiversity

conservation especially. For example, Oscar de Beaux, also a pioneer in conservation biology (cf. Gippoliti 2006), rejected the classification of the wild goats of the genus *Capra* proposed by Ellerman and Morrison-Scott (1951) explicitly, because this excessive lumping approach undermined his efforts to protect pure stocks of the taxa of *Capra* across the Palearctic Region (de Beaux 1956: 125).

It cannot be a coincidence that a well-known early failure of ‘genetic rescue’ involved three taxa of the genus *Capra* (*Capra ibex* Linnaeus, 1758, *Capra nubiana* F. Cuvier, 1825 and *Capra hircus* Linnaeus, 1758) released on the Tatra Mountains (Turček 1951, Templeton 1986). This example illustrates how a simplified classification of a species complex may lead to ill-conceived actions of genetic rescue, e.g. in ungulates. Taxonomic revisions that integrate all available evidences including available museum specimens and genomic analyses should not be seen as counterproductive, but as fundamental to undergird conservation policies aiming to maintain the evolutionary potential of populations and species (Crandall et al. 2000).

RESULTS AND DISCUSSION

Overlooked diversity and conservation consequences

Revived interest in ungulate diversity has led to reappraisals of the diversity of the Perissodactyla and terrestrial Artiodactyla (for the name of the latter order we follow Asher and Helgen 2010). Surprisingly, these revisions revealed diversity at the species level that had been overlooked in earlier studies (see

examples in Groves and Grubb 2011, Gutiérrez et al. 2017, Gippoliti et al. 2018). Many of these recent taxonomic changes have raised subspecies of large mammals to species (often restoring their original specific status). The lesson of these recent revisions is that the real dimensions of ungulate diversity have yet to be determined with confidence, because a significant number of ungulate populations are still classified as subspecies of respective, geographically widespread species awaiting taxonomic revision. As exemplified by Common duiker, *Sylvicapra grimmia* (Linnaeus 1758), these candidates require the study of adequate materials to clarify if a given taxon deserves recognition as a full species, or represents a population that is only part of a larger cline.

These advances in knowledge of ungulate diversity have been criticised, however, on the grounds that ‘taxonomic inflation’ has negative impacts on conservation (Isaac et al. 2004, Frankham et al. 2012, Heller et al. 2013, Zachos et al. 2013a,b, Garnett and Christidis 2017). This criticism overlooks how taxonomic methodology defines this dynamic scientific discipline. A fundamental tenet of this modern methodology treats described taxa, species inclusive, as testable hypotheses (Lambertz 2017, Raposo et al. 2017). Although taxonomic recognition, preferably at the species level, is a prerequisite to assess conservation status by international and national bodies, the task of taxonomy extends beyond providing mere ‘stable’ species lists, even though the latter plaster over uncertainties to ease challenges for conservation decision makers.

In fact, when one actually examines the impact of taxonomic ‘splitting’ on conservation, purported negative effects turn out to be just the opposite, as foreseen by de Beaux (1956). Thus, Morrison et al. (2009: 3205) found that “all of the examples where taxonomic change helped [species] protection involve splitting”, upending the argument of Isaac et al. (2004) against taxonomic inflation. This contrast highlights the negative effects of Gippoliti et al.’s (2018) taxonomic inertia.

Partially, widespread support for restocking as a mainstream action of conservation is facilitated by the persistence of the concept of the polytypic species, which is the operational equivalent of the Biological Species Concept (see Mayden 2002). In practice, the dominant approach has characterized polytypic species on their (apparent) phenetic similarity (cf the Phenetic Hypothesis, Cotterill et al. 2014). As exemplified in its applications to vertebrates, polytypic classifications lump phenotypically similar populations into a single ‘species’ (cf Burbrink et al. 2000, Cotterill 2003, de Queiroz 2007, Jolly 2014, Oláh et al. 2018). Although the polytypic species concept might inadvertently identify evolutionary lineages (a temporal series of populations connected by a continuous line of descent from ancestor to descendent), it fails in classifying them as the species that are the central currency informing conservation policy. Alongside many cases of cryptic species of small mammals (e.g. *Microcebus* sp. in Hotaling et al. 2016; *Myotis lucifugus* in Morales and Carstens 2018), the obsolete taxonomy of ungulates undermines core conservation goals, because a high proportion of evolutionary lineages are dismissed as ‘only subspecies’.

In combination, taxonomic inertia with classifications that lumped phylogenetic species into a polytypic species, favoured translocation of exotic stocks purporting to ‘enhance’ the value of game hunting areas or tourist attractions or as conservation measure. For example, importations of red deer (*Cervus elaphus* Linnaeus, 1758) from parts of continental Europe (mainly Germany) to Great Britain, Italy (and other extralimital habitats) aim to ‘upgrade’ supposedly inferior stocks to provide better hunting trophies (Frantz et al. 2006). The underlying rationale is if two populations are the same species (apparently), there would be no reason not to mix them: either to improve trophy quality in game animals, or in case of conservation, rescue putative genetically impoverished populations. The ensuing admixture has disrupted

phylogenetic structure in several ungulate taxa, including cryptic evolutionary lineages consisting of local endemics, which most likely were best adapted to local conditions. Nearly 40 years ago, Greig (1979) warned of the dire consequences of translocations, especially on North American and South African ungulate diversity. His advice has been ignored. In the last decade, again, concern has increased over the intentional or unintentional mixing of ungulate lineages in South Africa (Spear and Chown 2009, van Wyk et al. 2017), to the point where the IUCN/SSC Antelope Specialist Group has published a statement against the genetic manipulation of antelopes (IUCN SSC Antelope Specialist Group 2015).

Similar cases of misguided admixtures have ensued: wapiti *Cervus canadensis* Erxleben, 1777 imported into Europe, Siberian roe deer *Capreolus pygargus* (Pallas, 1771) into Central Europe, and Alpine chamois *Rupicapra rupicapra* (Linnaeus, 1758) into Slovakia (Linnell and Zachos 2011, Ferretti and Lovari 2014), along with impacts on South Italian wild boar *Sus scrofa* Linnaeus, 1758 in southern Italy (Maselli et al. 2016). Here, we highlight the relative lack of concern over these ‘melting-pots’ of human induced genetic diversity, which might lead to genetic and biogeographic homogenization. The conservation impacts of such admixtures are too often unrecognized; they can lead to losses of local adaptive traits, which are swamped by introgression. Notwithstanding belated concerns over alien species (McGeoch et al. 2010), the damages done through the extirpation and/or mixing of local populations of ungulates, with an increase of homogenization at both biogeographic and taxonomic level remain widely neglected in conservation concerns and policies. After all people may be happy to see red deer, even if that particular ‘red deer’ is not the same that lived there historically.

Genetic rescue needs robust evaluations

Under certain conditions, mixing stocks of threatened species can increase the chances for

species recovery (e.g. Cook and Sgrò 2017, Mills 2017, Supple and Shapiro 2018). Such ‘genetic rescue’ can mitigate the negative effects of inbreeding and low genetic diversity: reversing these impacts by crossing at-risk populations (Frankham 2015, Ralls et al. 2018). The basis for this ‘evolutionary approach’ (Weeks et al. 2011) is the empirical evidence that mixed populations show increased genetic diversity, which counteracts possible negative effects of homozygosity, and hybrids sometimes exhibit higher vigour compared to their parent populations (well known as heterosis in plant and animal breeding). Therefore, in the case of translocations, restoration efforts for an endangered population should maximize genetic diversity and adaptability (Sgrò et al. 2011). The counterargument invokes the problems of outbreeding, especially in small populations where genetic purging can be expected to have taken place, as this can severely hamper long-term survival of the population (Peer and Taborsky 2005). If an overly simplified taxonomy is applied, i.e. if two or more evolutionary lineages (gene pools) are classified as the same taxon, despite the risks that these populations actually have independent evolutionary histories, interbreeding of these lineages (attempting their genetic rescue) may create new problems, such as outbreeding. Similarly, the reintroduction of confiscated and displaced animals without knowing their geographic provenance and phylogenetic relationships risks outbreeding and introgression (Banes et al. 2016). As discussed by Tallmon et al. (2004) and Hedrick and Garcia-Dorado (2016) these outcomes are comparable to negative effects of hybridization (Björklund 2013). Moreover, Gippoliti (2018) recently highlighted that the available evidence of the benefits of ‘genetic rescue’ is ambiguous. Actually, most, if not all, of these positive cases involve the mixing of individuals belonging to the same subspecies, as the Mexican wolf *Canis lupus baileyi* Nelson and Goldman, 1929.

Furthermore, the mixing of stocks, which actually qualify genetically as two (or

more) distinct evolutionary lineages, creates a chimeric entity, which never existed in nature; and many such chimeric hybrids may actually be less adapted to local conditions. Although a complete overview is lacking, there are several case reports of females of a small-sized subspecies that encounter severe problems during pregnancy or parturition if they conceived from a male of a larger-sized subspecies because of the large size of the hybrid calf (Turček 1951, Galindo-Leal and Weber 1994). Risks of such deleterious effects should rank high in assessments of translocation plans - whether for reasons of conservation or selective breeding by game-ranchers seeking more valuable hunting trophies. These philosophies concerned over outbreeding versus inbreeding, respectively, underscore a deep tension between prevailing, and prominent, conservation policies (including relevant IUCN guidelines on translocation projects) and what has been rather preemptively defined as an 'evolutionary' approach to conservation (Mace and Purvis 2008, Cook and Sgrò 2017).

We note prominent historical cases among ungulates where the conservation of very small populations has frequently been successful, despite whether inbreeding did or did not occur, both in situ and ex situ situations. These cases include: Alpine ibex *Capra ibex*, Père David's deer *Elaphurus davidianus* Milne-Edwards, 1872, European bison *Bos bonasus* (Linnaeus, 1758), Southern white rhinoceros *Ceratotherium simum* (Burchell, 1817) and, more recently, Apennine chamois *Rupicapra ornata* Neumann, 1899. The Soemmering's gazelle *Nanger sommeringii* (Cretzschmar, 1828) offers an interesting comparison of results between the two opposing views. The small captive population of unclear ancestry shows poor breeding results, which have been explained, both, as consequence of inbreeding and outbreeding depressions (Steiner et al. 2016). Interestingly, Dahlak Kebir Island, in the Dahlak Archipelago, off the coast of Eritrea, in the southern Red Sea, is inhabited by a population of Soemmering's gazelles of

significantly smaller body size (Chiozzi et al. 2014). Although its origin is poorly known, and despite periodic die offs under harsh environmental conditions (genetic bottleneck) and an assumed high degree of inbreeding, this distinctive taxon is currently flourishing on the island with an estimated 4000-4500 individuals (Mallon 2015). Ironically, this endemic population is still an undescribed taxon. Moreover, a recent genomic study of the small extant population of mountain gorillas *Gorilla beringei beringei* Matschie, 1903 found that a population decline has resulted in extensive inbreeding (individuals are typically homozygous at 34% of their sequences, Xue et al. 2015). This, however, lead to the purging of severely deleterious recessive mutations from the population.

We do not argue that problems of inbreeding are not real and can have detrimental effects on small populations. Nevertheless, the examples identified among ungulates question the scientific integrity of intervention policies promoting genetic exchange among 'subspecies' (actually putative species). These policies include actions to rescue a small population. In any case, a robust population genomic analysis should be carried out before respective gene pools of threatened species will be manipulated for the sake of conservation management (e.g., Supple and Shapiro 2018). As Ralls et al. (2018) pointed out, if the risk of outbreeding depression is low, the default should be to evaluate whether genetic rescue will be possible and beneficial, rather than inaction. However, lumping diverging populations into one taxon, and then invoking such taxonomy as the solely argument for restocking and genetic rescue demands serious questions – not least on the grounds of scientific credibility and public funding.

We do not dismiss the importance of gene-flow for the maintenance of population viability, but we argue that all planning, and ensuing actions, in biodiversity conservation remain centrally reliant on the scientific characterization of species. This dependency of scientific decisions on robust taxonomies

underscores the role of the taxonomist to revisit and revise key populations: utilizing the maximum of available study materials, especially museum collections, and available technology. An example of integration between conservation practice and taxonomy is the case of bighorn sheep *Ovis canadensis* Shaw, 1804, where genetic rescue is commonly implemented to improve long-term prospects for small isolated populations in the deserts of the South-West of USA (Hedrick and Wehausen 2014), but utilising only animals of the same taxonomic unit (Buchalski et al. 2016). At the other extreme, there are the problems incurred where management practices rely on outdated taxonomies, which have never been investigated and revised critically. In such cases misinformed translocations may either fail and/or reshape the gene pools of evolving lineages unnecessarily.

The ‘subspecies’ problem and genetic rescue

Modern taxonomy has left behind the polytypic species classification founded in the Biological Species Concept, and its singular criterion that ‘good species do not interbreed’. Therefore, discriminating species and subspecies on the basis of whether they interbreed is untenable (Gippoliti et al. 2018, and references therein). Hybridization between universally accepted species in nature and under semi-natural conditions is a common phenomenon, e.g., plains zebra *Equus burchelli* (Gray, 1822) hybridize with Grévy's zebra *Equus grevyi* Oustalet, 1882 in Laikipia, Kenya, and with Cape Mountain zebra *Equus zebra* Linnaeus, 1758 in Mountain Zebra National Park, South Africa; blue wildebeest *Connochaetes taurinus* (Burchell, 1823) and black wildebeest *Connochaetes gnou* (Zimmermann, 1780) on private game farms in South Africa (Cordingley et al. 2009, Grobler et al. 2011, Dalton et al. 2017).

Another example of the taxonomy of wild goats is instructive of an early case of cryptic diversity in threatened ungulates was recognized in the early 20th century, but

ironically disregarded by conservation planners. Italian systematist Lorenzo Camerano (1917a: see also Gippoliti and Robovský 2018) argued that the subspecies category may be useful to focus attention on underappreciated geographical variation in species complexes. One of his most prominent studies (Camerano 1917b), on Iberian ibexes, challenged the earlier taxonomic interpretation by Cabrera (1911), who had recognized a single species, *Capra pyrenaica* with four subspecies. Utilizing cranial characters, including the shape of the nasals and palaeontological findings, Camerano reached the conclusion that two species can be recognized, *Capra pyrenaica* and *Capra hispanica* Schimper, 1848. Moreover, these two ‘primary species’, as he called them, comprised three ‘subspecies’ with intermediate characters (*lusitanica*, *victoriae*, and *cabreræ*). Today we can only speculate how the decline of the now extinct bucardo *Capra pyrenaica* might have been mitigated, had its uniqueness been accepted long before confirmation by genetic data (Manceau et al. 1999, Ureña et al. 2018). Incidentally, to our knowledge, no attempt has been made to select individuals for reintroduction into the Pyrenees from populations phylogenetically closest to the extinct *C. pyrenaica*.

Nevertheless, recent appraisals of ibex diversity in the Iberian Peninsula continue to ignore evolutionary lineages. For example, Angelone-Alasaad et al. (2017) recovered unexpectedly high genetic differentiation (reliant on microsatellites) between two populations (Sierra Nevada and Maestrazgo) that belong to the same nominal subspecies, *Capra pyrenaica hispanica*, one of which presumably represents an unrecognized cryptic evolutionary lineage. Instead, these authors presumed the genetic pattern to be the result of strong genetic drift due to severe bottlenecks in the studied populations, exacerbated by the progressive destruction of natural habitat, disease epidemics, and/or uncontrolled hunting. Angelone-Alasaad et al. (2017) did not discuss nor question the possibility that the ‘orthodox taxonomy’ (even at a subspecific level) is

invalid. Beyond the status of the data and methods available a century ago (when Cabrera [and Camerano] reported on these populations), the prevailing uncertainty highlights a lack of concern about the persisting absence of their taxonomic revision of ibex diversity (Gippoliti et al. 2018, Gippoliti and Groves, 2018).

The diversity of the circumboreal deer of the genus *Rangifer* species complex serves as the apt case study of the negative impacts of overly simplified taxonomy on conservation. The genus has been generally treated as monospecific, with four subspecies recognised in North America (Banfield 1961). Geist (2007) considered that this taxonomy oversimplified. It lumped taxa together into a false species, thus overestimating the population size of true 'woodland caribou' *Rangifer tarandus caribou* (Gmelin, 1788). Considering the decline of several populations in Canada, and the need to translocate stocks for conservation reasons, it is no surprise that several authors had questioned the value of taxonomic units to this end (Miller et al. 2007). Attempts to halt the decline population of the montane ecotype of 'woodland caribou' of British Columbia (putative *Rangifer montanus* Seton, 1899) failed, because relocated woodland caribous did not adapt to local conditions and failed to breed with the native animals (Leech et al. 2017). This conservation failure is unfortunate, not least, it highlights the taxonomic errors in the current conception of *Rangifer* diversity. Strangely, nobody appears to have identified the primary action to place caribou conservation on a solid evolutionary foundation: undertake a taxonomic revision utilising the ESC, and thus test if *Rangifer* is a monospecific genus through integrative taxonomy.

It is instructive to frame the tension over inbreeding versus interbreeding in conservation in a wider context. Seeking out conservation strategies for populations of management concern, these two schools of argument invoke tenets in population genetics versus evolutionary theory. The one overlooks the priority to minimize the risks and costs of

ignoring the historical origins of evolutionary lineages. These population geneticists worry that human-induced habitat fragmentation exacerbates genetic drift in taxonomically uniform populations ('pseudo-speciation'). Conversely, comparative biologists argue that conservation planners cannot continue to overlook the phylogenetic distinctiveness represented in extant lineages. This strategy underscores attention to cryptic species (too often overlooked historically). Several reasons underline the strong case that any conservation policy that ignores phylogenetic distinctiveness is more than theoretically weak. Serious problems can result where conservation action plans misconstrue diversity at the population level, especially where distinct species interbreed. For example, the argument by Harley et al. (2016) to 'rescue' the Nile rhinoceros *Ceratotherium cottoni* (Lydekker, 1908) by interbreeding with *Ceratotherium simum* is misguided, because the subspecies classification of white rhinos had been refuted by the morphological and genetic evidence analysed in a phylogenetic framework (Groves et al. 2017). Regrettably, the 'agony of choice' will demand now to save the maximum we can of the genome of the Nile rhinoceros whatever his taxonomic rank actually is (Hildebrandt et al. 2018).

CONCLUSIONS

We appreciate that characterization of some species might never approach unanimity (whatever species concept is used), particularly where variation manifests in clines or hybrid zones where it is difficult to find unambiguous evidence of the individuated lineage. Moreover, by its intrinsic nature, science is an ongoing endeavour. Nevertheless, we urge wildlife biologists to place conservation theory and practice on the foundations of modern taxonomic approaches built on the concepts and theory of phylogenetic systematics (Wiley 1978, Mayden 2002). Modern taxonomy has matured to rely centrally on the phylogenetic lineage approach founded, in turn, on the

ontology of the Evolutionary Species (= General Lineage Concept); and it is this framework of the Consistent Solution (Cotterill et al. 2014) that conservation planners should structure any actions of genetic rescue (founded in genomic analyses of populations of concern).

Although wild ungulates have had a long history of human management and translocations, similar problems impact many other species, including other vertebrates. For example, in freshwater fish homogenisation of fish faunas is a global problem. Due to deliberate and undeliberate translocations and introduction of non-native species by humans and extinctions freshwater fish diversity of different river systems tends to become more and more similar (Taylor 2004, Villéger et al. 2015, Sommerwerk et al. 2017). Similarly, for conservation reasons, the taxonomic/genetic origin of translocated birds is too often neglected with negative results (Olsson 2007). For example, the Buttonquail, *Turnix sylvaticus sylvaticus* (Desfontaines, 1787) - highly endangered in the Mediterranean Region - is clearly distinct from the subspecies found in SubSaharan Africa *Turnix sylvaticus lepurana* (A. Smith, 1836) (Pertoldi et al. 2006, Gutiérrez et al. 2011). Any attempts at its rescue in the Mediterranean region by introducing the sister taxon would *de facto* introduce a new evolutionary lineage. A probably useful source population to reintroduce the buttonquail into its formerly southern European range would be the small population at the west coast of Morocco, which appears to be affiliated with the same lineage as the extinct European form (Pertoldi et al. 2006, Gutiérrez et al. 2011). Impacts of poorly informed attempts at genetic

rescue also appear widespread among amphibians (Dubois 2006). Recent integrative research showed that the release of farm breed individuals of the iconic Chinese giant salamander *Andrias davidianus* (Blanchard, 1871) has manifested in significant threats to the cryptic diversity of the genus, now known to comprise at least five species (Yan et al. 2018). Similarly, the integrity of divergent lineages of fishes was also negatively impacted by restocking activities (cf. Marie et al. 2010).

We note, finally, how updated taxonomic revisions, increasingly supported by genomic information that resolve species diversity (concomitantly reducing recognized subspecies) reveal overlooked geographical affiliations among the real evolutionary lineages. These advances in the taxonomic knowledge of ungulates can only bring positive (and overarching) benefits to biodiversity conservation, whilst guiding translocations in their constructive role in an integrated strategy.

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AUTHOR CONTRIBUTIONS

All four authors wrote and contributed equally to the paper.

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