

Chapter 16 Cryptic Problematic Species and Troublesome Taxonomists: A Tale of the Apennine Bear and the Nile White Rhinoceros

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16.1 Introduction

Among a broader definition of 'problematic wildlife' (Angelici 2016), we think that a special section should be reserved for those 'taxa' whose conservation strategies depend upon the taxonomic status accorded to them by the scientific community. In recent decades, it has often been argued that a taxonomy of large mammals based on the BSC (biological species concept) is favourable to conservation policies as it allows artificially mediated gene flow among distant populations belonging to the same species (Frankham et al. 2012; Heller et al. 2013; Zachos et al. 2013; Ralls et al. 2018). Linked to this view seems to be the hypothesis that conservation problems mainly concern the genetic viability of small populations that remain isolated owing to human-caused destructive behaviours such as hunting and habitat alteration (small population paradigm, cf. Caughley 1994). However, a finer definition of 'evolutionary species units' can inform a conservation strategy that might make sense if past unique evolutionary trajectories in populations are being conserved (Weeks et al. 2011). Weeks and co-authors are also concerned that if these populations are not really 'unique' at all but that they are managed as distinct units, we may increase their risk of extinction due to reductions in genetic diversity and loss of population fitness. Actually we share this concern and, additionally, we do not wish to allocate precious resources to 'phantom taxa' (cf. Gippoliti and Amori 2002a) when there is so much neglected biodiversity nor is it our wish to let species vanish because of depauperate genetic pools.

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Previously we advocated integrative taxonomy as the way to identify evolutionary species beyond the sole use of neutral molecular markers to identify evolutionary lineages in ungulate mammals (Groves and Grubb 2011; Cotterill et al. 2014; Groves et al. 2017; Gippoliti et al. 2018b). Users of taxonomic data are all too often ignorant of how imprecise or wrong current taxonomies can be and consequently how dangerous it is to utilize current taxonomy as a yardstick to generalize about issues such as inbreeding and outbreeding depression, especially in the absence of taxonomic revisions in the last half a century (Goldstein et al. 2000).

Supporters of 'genetic rescue' (e.g. Vander Wal et al. 2013) credit this technique with the restoration of populations of cougars in Florida (*Puma concolor*), bighorn sheep (*Ovis canadensis*) and adders (*Vipera berus*). We note that the last two cases refer to translocation between the same putative subspecies. In the case of the Florida cougar, generally considered a distinct subspecies, *Puma concolor coryi*, it has been re-stoked with individuals belonging to the Texas subspecies *P. concolor stanleyana*. It seems that all North American forms of cougars have a recent origin, and genetic diversity among subspecies is low (Culver et al. 2000) so the risks of outbreeding depression (Templeton 1986) in this case was probably low (Hedrick and Fredrickson 2010). But this is a much greater risk in the case of evolutionary species that are artificially lumped into 'biological' species (see below), or little-known subspecies that have never been thoroughly taxonomically revised in recent decades (cf. Groves et al. 2017).

Outbreeding depression indicates a fitness reduction following hybridization (Templeton 1986). According to the so-called Dobzhansky–Muller model, isolated populations gradually accumulate neutral or advantageous mutations over time, and selection for positive epistasis may result in the development of unique coadapted gene complexes within each isolated population (Edmonds 2007). Thus, when mating occurs between populations, segregation and recombination can break up these coadapted gene complexes and bring together mutations that have not been 'tested' together and potentially have harmful effects (Turelli et al. 2001). This is not to deny the potential evolutionary importance of hybridization that has influenced even our own species (Harris and Nielsen 2016) but rather to highlight our scepticism towards a single cure – genetic rescue – which has been studied in the laboratory but has not been tested in the field.

As a case in point, we draw attention to one successful conservation story: the Arabian oryx *Oryx leucoryx*. After the species was saved from extinction by captive breeding and reintroduced into protected areas located in its original homeland, signs of outbreeding depression were discovered in the surviving population (Marshall and Spalton 2000; Ochoa et al. 2016). Why should this be? It is of some interest that in 1934 Pocock described a subspecies, *Oryx leucoryx latipes* from Wadi Ghudun, Southern Arabian Peninsula (now in Oman), remarking how the skin he received showed 'markedly wider and differently shaped hoofs' compared to all other available specimens then in the British Museum (Pocock 1935: 464). He compared the hoofs to those of *Addax nasomaculatus* and suggested that this would be a character of specific relevance resulting from adaptation to loose sand. Considering that he had only one specimen at hand, he preferred to name a new subspecies

merely 'to draw attention to its interest' (Pocock 1935: 466). Regrettably, the age of 'taxonomic inertia' was beginning at that time and Ellerman and Morrison-Scott (1951: 386) simply commented, 'We regard this form as of doubtful validity'. No surprise then that most present-day researchers (Ochoa et al. 2016) dismissed the hypothesis that there was any ancient isolation in *Oryx leucoryx* driven by geographic and ecological factors. Today we have the technology to test if the Arabian oryx shows cryptic historical patterns of genomic and taxonomic diversity. Specifically, a genomic study should analyse not only available museum specimens from the historic range but the extant captive population – including the founders – to ascertain if two or more cryptic evolutionary units have effectively been swamped together.

16.2 Taxonomic Oversimplification

For most of the twentieth century, under the BSC with its acceptance of a plethora of polytypic species, most described taxon names were synonymized or, at best, accepted to be of subspecific validity. But, again, this was often accomplished without the help of a true taxonomic revision (e.g. critical examination of most available museum specimens and type specimens at the end to assess taxonomic variability in a taxonomic group (genera, species)). Natural history museums and traditional taxonomists had in the meantime fallen under the spell of the Modern Synthesis, or rather of what was interpreted as its taxonomic corollary, especially in Western Europe (Gippoliti and Groves 2018). This process of simplification is described below by one of the fathers of the modern synthesis, Ernst Mayr (1982): 'While the morphological criterion of intergradation had previously been the exclusive subspecies criterion, "geographical representation" now became the yardstick. As Stresemann (1975) has described so well, every isolated 'species' was now scrutinized for the possibility that it was simply a 'geographical representative' of some other species, in which case it was reduced to the rank of subspecies. The subspecies was subsequently defined as a member of a polytypic species, not simply as a 'slightly different' local population. The new way of looking at geographical isolates, particularly the downgrading of every isolate to subspecies rank, even if these were not clearly connected by intermediates, resulted in an extraordinary simplification of taxonomy at the species level. Among the 607 species of North American birds alone, 315 taxa that had originally been described as full species were subsequently reduced to subspecies status. The newly recognized polytypic species were much more distinct, real entities of nature compared to the purely morphologically defined 'species' of the 1880s. Morphological difference was replaced as species criterion by reproductive isolation' (Mayr 1982: 593–594).

Another consequence of this process is that under the same category of 'subspecies', there can now be found a heterogeneous array of evolutionary stages (Gippoliti and Amori, 2007). True species has been artificially lumped into a polytypic species, while other subspecies are essentially points on a cline. 'In retrospect, it has become clear not only that many of the so-called subspecies described from the 1920s to the 1940s did not differ in the slightest, but also that the recognition of minutely differing populations served, in most cases, no good purpose' (Mayr 1982: 594). This has important consequences because many researchers assign a spurious objectivity even to the subspecies category, lamented by Lorenzo Camerano as long as a century ago (Camerano 1916).

Interestingly, it seems that the oversimplification of taxonomy through the polytypic species concept has found a use in at least one other field of environmental conservation: ecological connectivity. Human-induced habitat degradation and fragmentation is certainly one of the major causes of a population's loss of viability (Lindenmayer and Fisher 2007), so the maintenance or creation of a network of ecological corridors has often become one of the main goals of wildlife conservation, although the validity of this approach has been rarely tested in a scientific way (Gippoliti and Battisti 2017). What is more interesting from our perspective is that isolated populations of large mammals have almost invariably been assumed to be the result of historically human-mediated extirpation of connection between populations by either direct persecution or by habitat degradation. This belief is repeated in almost all papers dealing with molecular aspects of large mammals (i.e. Angelone-Alasaad et al. 2017), even in those cases where genetic or morphological data could in fact support (or at least be tested) a different scenario, namely, that a given population was already distinctive (thus isolated) before the peak of anthropogenic destructive activities (see also Sexton et al. 2014).

16.3 Troublesome Taxonomists

Rojas (1992) was among the first to recognize the existence of a problem in the application of different species concepts for biodiversity conservation policy. Much earlier, the pioneer conservationist and mammal taxonomist Oscar de Beaux (Fig. 16.1; Gippoliti 2006) was probably the first to recognize how the 'new taxonomy' posed more than a challenge for biodiversity conservation. He dedicated the last years of his life to a monograph on the wild goats of the genus *Capra* (de Beaux, 1956), in which he refuted the taxonomic vision proposed by Ellerman and Morrisson-Scott (1951) which, in that specific case, was even less simplified than those already advanced by Schwarz (1935). As early as 1930, when de Beaux published his *Etica Biologica*, later translated into English (de Beaux 1932) and cited by Aldo Leopold (Leopold 1933), he stressed the importance of preserving the results of evolutionary history. De Beaux included among the conservation priorities the distinctive populations of Maremman roe deer, those of the Gargano and Calabria (Southern Italian Peninsula), the Maremman wild boar and those living in Southern Italy even if then unstudied scientifically (de Beaux 1930).

It is perhaps no coincidence that one of the most known (and unsuccessful) cases of *ante-litteram* genetic rescue/translocation involved members of the genus *Capra*. An assemblage of *Capra* taxa, *Capra ibex*, *Capra ibex* x *Capra nubiana* and *Capra*

Fig. 16.1 Oscar de Beaux



aegagrus, which at that time were regarded as members of one polytypic species, were released on the Tatra Mountains, but owing to the lack of the right birth seasonality and lack of human care during the Second World War, the experiment failed (Turček 1951). This remarkable early unsuccessful example, fuelled by the excessive synthetic approach of Schwarz (1935), is a powerful reminder that species cannot be discriminated on the basis of breeding compatibility and, if this is done, there would be some grave problems in conservation biology. Interestingly, de Beaux believed humans had a moral duty to not interfere with the existing diversity pattern well below species level, an issue that is critically reviewed by Rohwer and Marris (2016).

We have observed that after decades of 'taxonomic inertia', it is not easy to propose 'revolutionary' changes in the way people see the world. The revisionary work on the world's ungulates by Groves and Grubb (2011) was often received with hostility and the criticisms often failed to focus on true scientific issues. But even in more parochial (but yet important) issues, we see how difficult it is to open a frank discussion among different researchers and disciplines. Regarding the conservation issues of the so-called woodland caribou Rangifer tarandus caribou, only the single authoritative voice of Valerius Geist (Geist 2007) called for an urgent revision of the taxonomy, an issue that has so far remained unheard. How neglected taxa can become critical for biodiversity conservation is demonstrated by the case of the Bale monkey Chlorocebus djamdjamensis in Ethiopia. Ignored by most mammalogists and primatologists - with the exception of Pierre Dandelot - during the twentieth century, this species was first 'rediscovered' in the Harenna Forest by one of us (Carpaneto and Gippoliti 1994) who reviewed its taxonomic history and highlighted that this was a uniquely mountain bamboo-forest subspecies of the otherwise savannah-living aethiops complex. Subsequently, both Kingdon (1997) and Groves (2001) raised *djamdjamensis* to full species status. Further genetic data established that under the name *djamdjamensis* two genetically distinct populations exist (Haus et al. 2013), one of which shows traces of extensive introgression with other *Chlorocebus* species. Further research has confirmed the distinctiveness of the two ESUs (Mekonnen et al. 2018). What is of relevance is that the presence of an endemic primate species made international funding available for research and conservation on this highly restricted species, making it an effective umbrella and flagship species for montane forest conservation in Bale and Sidamo regions of Ethiopia (Mekonnen et al. 2012, 2017), a habitat so far neglected by conservationists.

16.4 History of Translocations in Conservation Biology

From a conservation biologist's perspective, the era of taxonomic inertia opened the door to a number of appealing and apparently successful conservation operations, such as the translocation of wildlife species in regions from where they had been long extirpated. In 1976 WWF Italy organized a meeting on Reintroductions: techniques and ethics (Boitani 1976), from which, however, taxonomic considerations were almost completely absent. The attached 'manifesto on animal re-introductions' specified that, in cases of restocking, '...the animal must be of the same race as those in the population into which they are released'. In addition, the manifesto specified that '... the animals reintroduced must be of the closest available race to the original stock' (Boitani 1976: 300). Given that we may consider the term race – in this instance anyway - a synonym of subspecies, the document is in agreement with the attitude of past times, which assumed that all we need to know about subspecific variation was already known and available to wildlife conservationists. We note that many researchers have always emphasized the importance of maintaining unaltered existing patterns of geographic variation inside biological species. In the case of Caprinae, it has been stressed that a subspecies extinction by humanmediated introgression is a really extinction, and proposed conservation recommendations are at the subspecies level (cf. Shackleton and Lovari 1997). In 1987 an IUCN Statement on the Translocation of Animals was produced (IUCN 1987) and in 1988 an IUCN/SSC Re-introduction Specialist Group was established that published guidelines for re-introductions in 1998 (IUCN 1998). In 1999 Seddon and Soorae (1999) proposed guidelines for subspecific substitutions in translocations, when the original subspecies is extinct.

According to the IUCN/SSC (2013), founders should show characteristics based on genetic provenance and on morphology, physiology and behaviour that are assessed as appropriate through comparison with the original or any remaining wild populations. In some cases the original species or subspecies may have become extinct both in the wild and in captivity. A similar, related species or subspecies can be substituted as an ecological replacement, provided that the substitution is based on objective criteria such as phylogenetic closeness, similarity in appearance, ecology and behaviour to the extinct form. Regrettably, extinction of a 'subspecies' is not a rare phenomenon and a reasonable replacement, as we will see, is not always possible as we deal, in fact, with unique lineages adapted to very specific ecological and geographical niches. The whole issue is much more complicated (Gippoliti et al. 2018a, b), but we would highlight here that the abandonment of the subspecies category as observed in some IUCN Specialist Groups will certainly have consequences for translocation/restocking policies.

16.5 The Nile or Northern White Rhinoceros

Groves et al. (2010) revised the taxonomy of living *Ceratotherium* (white rhinoceros) and concluded that the two living taxa are best treated as separate species, the southern white rhino (SWR) *Ceratotherium simum* in Southern Africa and the northern (or Nile) white rhino (NWR) *Ceratotherium cottoni* in Central Africa.

IUCN's African Rhino Specialist Group (AfRSG) reacted negatively to this proposition:

This conclusion is being contested by, amongst others, African rhino genetics expert Colleen O'Ryan who has informed the AfRSG that she and her colleagues are working on a detailed rebuttal of Groves et al.'s paper based on findings derived from larger sample sizes, and using what she feels are more appropriate genes (Brooks 2010: 14).

This represent an obvious misunderstanding, as no scientist would work on an already predetermined rebuttal, and no geneticist would refer in such a context to any gene as 'more appropriate' than any other. Nonetheless, O'Ryan's research group has more recently conducted such a test, sequencing the entire mtDNA genomes of four NWR and three SWR (Harley et al. 2016), and compared them to Rhinocerotidae from GenBank as well as selected outgroup taxa, including mtDNA genomes of modern Homo sapiens and what they referred to as Homo sapiens neanderthalensis and Homo sapiens denisova (that is to say, the Late Pleistocene Neanderthal people of Europe and western Asia and the mysterious Denisovans, known only by a tooth and a manual phalanx). The results corroborated the main findings of Groves et al. (2010), namely, that NWR and SWR are reciprocally monophyletic (with 100% support). Despite this, Harley and colleagues disputed their status as separate species, the main arguments being that, first, accepting them as different species would be 'a problem for conservation' (Harley et al. 2016: 1286) because they maintained that if some of the genes of NWR were to be saved, the only hope seemed to be that the last survivors should be interbred with SWR. Their second argument was that the genetic distances (p-distances) between SWR and NWR were less than those between modern humans and either Neanderthals or Denisovans. The first point comes up against the probability of outbreeding depression in any hybrids; as for the second, Harley et al. (2016) were under the impression that Neanderthals and Denisovans are considered subspecies of *Homo sapiens*, which is not the case generally. They likewise claimed that the PSC 'would also lead to the requirement for *H. sapiens* to be divided into a large number of separate species' (Harley et al. 2016: 1290); this frumpy statement has been dealt with by Groves (2012, 2014) and Groves & Robovský (2011).



Fig. 16.2 Part of the Nile white rhinoceros group at Dvur Kralove Zoo in 1991. (Photo S. Gippoliti)

In summary, the combined evidence for unambiguous diagnosibility of *Ceratotherium cottoni* versus *C. simum* is beyond doubt. The two are (or were, alas) clearly individuated evolutionary lineages. Yet the fact that it was almost universally recognized only as a subspecies of *C. simum* and that the latter taxon flourished under strict protection (Rookmaaker 2000) makes awareness of the importance of conserving the Nile white rhinoceros (*C. cottoni*) less urgent. Although first imported to zoos in 1950 (much earlier than its southern congeneric), the captive population of the NWR was fragmented among a number of zoos that kept pairs that never breed in such a deprived social condition.

Only Dvur Kralove Zoo (in then Czechoslovakia) (Fig. 16.2) operated its own innovative acquisition programme that in retrospect offered at least a chance to create a self-sustaining ex situ population. In 1975 a small herd was captured in South Sudan, before the poaching rise after 1980 (Hilmann-Smith et al. 1986). The history of the status of the species in the Garamba National Park (Democratic Republic of Congo) (Fig. 16.3) was summarized by Hilmann-Smith et al. (1986). Interestingly, differences between NWR and SWR were already evidenced at the time: 'The skull shape is distinct in the field, and the head is held higher than in southern whites. Body proportions are also different, with the northern white rhinos tending to be shorter, and there are almost certainly *ecological* and *behavioural* differences between the two subspecies' (Hilmann-Smith et al. 1986: 20). We evidenced some words in italics because too many laboratory researchers and zoologists, at most familiar with one studied population, are unaware of how subtle ecological conditions coupled with geographic isolation may produce phenotypically different populations, which is quite unappreciated to the unexperienced eye.

Groves et al. (2017) reviewed the issue and another important aspect is that while in Southern Africa the SWR was sympatric with the black rhinoceros *Diceros bicornis*, this was not the case in Central Africa. This suggests that the NWR could be less strict grazers than the SWR. Interestingly, differences between the two taxa were also found when studying the social behaviour of captive rhinoceros and their



Fig. 16.3 Nile white rhinoceros in the Garamba National Park. (Photo Francesco Germi)

vocalizations (Kuneš and Bičík 2002; Cinková and Policht 2014. It seems that either the wish of the Democratic Republic of Congo (formerly Zaire) to maintain in situ a 'national treasure', and the fall of the ark paradigm in zoos' conservation work (Gippoliti 2011) and the adopted taxonomy conspired to halt the preparation of a 'plan B' for conservation of NWR. In some cases, political turmoil prevented the conservation of the last wild stronghold of the taxon. In a sense, the northern white rhino was first a victim of colonialism, 'scientific inquiry' and trophy hunting, with several hunters (some very famous such as Theodore Roosevelt, Winston Churchill, Frederick C. Selous, Vittorio Emanuele of Savoy-Aosta, Herbert Lang and Powell Cotton, obviously) bringing back not one or two but several specimens of these then - little-known species; 14 were taken by the Roosevelt expedition alone (Heller 1913). Later, it fell victim to post-colonialism and the decline of the new independent states, the heritage of colonialism. If we reflect on a history of now 60 years (Curry-Lindahl 1972) of political turmoil in Central Africa (and no bright future insight), we should ask ourselves if a strategy for this extraordinary species should have been developed when we had more options available. In 1976 the population in Garamba had risen to some hundreds of individuals and the capture of a small herd for a zoo should have had no effect on the wild population. Furthermore, it seems that no interest was shown in conducting surveys and eventually establishing protect areas in Chad and Central African Republic where the species was reported by local hunters (Owen-Smith 2013). Inevitably, geopolitics needs to be considered in conservation biology.

16.6 Apennine Bear

A similar case occurred in Italy, where the morphologically distinctive Apennine brown bear population has been generally treated just as a southern population of Ursus arctos. The history of the conservation of the Apennine bear (and of the Apennine chamois Rupicapra ornata Neumann, 1899) offers a powerful demonstration of how taxonomy can have a positive influence on wildlife conservation, as previously indicated by Cotterill et al. (2014) and Gippoliti et al. (2018a, b and references therein). When the Parco Nazionale d'Abruzzo was finally established in Central Italy, Altobello (1921) had just described the local bear population as a new subspecies, Ursus arctos marsicanus. Although some proposals for a National Park had been made before, safeguarding the stronghold of two unique mammal taxa the Apennine bear and the Apennine chamois, with their high touristic potential value – was a crucial element in the establishment of the park (Sipari 1926). The founder of the park, Erminio Sipari, discussed at length the taxonomic status of the Apennine bear, consulting not only with Altobello but with several other mammalogists such as Giuseppe Lepri, Enrico Festa, Paul Matschie and Theodor Knottnerus-Meyer (Sipari 1926). Altobello had only an adult female skull at hand (and two skulls of juveniles), so his original description (Altobello 1921) appeared so weak to Pocock (1932) that he relegated marsicanus to the synonymy of arctos. Already in Sipari's work new evidence was collected and Enrico Festa communicated to Sipari on the basis of material in the Turin University Museum that the superior profile of the skull in the frontal region was more convex than in Ursus arctos (Sipari 1926: 29). Ellerman and Morrison-Scott (1951) had no choice other than to follow Pocock's arrangement.

An original and (at the time) 'shocking' taxonomic view was offered by the paleontologist Sergio Conti. While studying and describing a particular 'variety' of cave bear from Liguria (North-West Italy) which he named Ursus spelaeus var. ligustica (Conti 1954), he made some comparisons with modern Alpine and the Apennine bears. After suggesting that his *ligustica* seems an intergrade between *spelaeus* and arctos, he also concluded that (having at hand an adult male skull of marsicanus) the Apennine bear was more related to *ligustica* than the Alpine bear, to the degree that he recognized marsicanus as a full species. Although Conti's sample was very limited, it is clear that the unique skull he had is fully representative of the Apennine population as a whole (Vigna Taglianti 2003; Colangelo et al. 2012) (Figs. 16.4 and 16.5) and his proposal should be taken seriously – evidently he had utilized the diagnostic version of the phylogenetic species concept (Wheeler and Platnick 2000) to identify evolutionary species. Differently from North America, in Europe the concept of 'subspecies' among mammalogists has received so far scanty attention. Although sometimes listed in the more accurate checklist (i.e. Amori et al. 1999), there has generally been no attempt to revise mammal taxonomies at the subspecies level, even utilizing the increasingly available data derived from phylogeographic studies. These data often indicated a more complex situation than showed by

Fig. 16.4 Dorsal view of the skull of the Alpine brown bear. (Photo Jacopo Conti)



Fig. 16.5 Dorsal view of the skull and mandible of the Apennine bear *Ursus arctos marsicanus* (photo Jacopo Conti)



traditional taxonomy and this is of potentially great importance as a basis for conservation strategies (Gippoliti and Amori 2002b).

The low level of genetic distinctiveness of Apennine bears from Balkan bears led Colangelo et al. (2012) to explain that the particular skull of the Apennine bear was mainly the result of genetic drift in a small population isolated for '240–720 years' from the Alpine population. We have already referred above to the 'belief' of humans, especially utilized in Europe, to be the only agent of range fragmentation and isolation. We also know that the southern European peninsula hosts a number of unique lineages that found refuge there during glacial periods (Bilton et al. 1998). In the case of the Apennine bear, early genetic data (mtDNA, microsatellites) are

not supportive of an ancient separation from other bears, yet a gene tree does not necessarily represent a species tree (Ferguson 2002). In addition, it is well known that shifts towards genome-wide single-nucleotide polymorphisms (SNPs) will be particularly useful to provide a comprehensive assessment of genetic distinctiveness and will allow more precision in targeting what deserves special efforts for conservation (Desalle and Amato 2017).

Can the presence of *spelaeus*-like characters in the skull and dentition of *marsicanus* (see also Capasso Barbato et al. 1993) really be explained by convergent evolution during 700 years of genetic drift? Or might it be possible that some *spelaeus* genes were present in the bear population south of the Alps, possibly due to an introgression episode (cf. Barlow et al. 2018)? These genes could be masked by other genes which got lost by genetic drift. So it should not be convergent evolution but the reappearance of a special set of genes due to genetic drift and/or introgression.

Gippoliti (2016) called for a taxonomic revision of the whole *Ursus arctos* complex and specifically considered the available evidence sufficient to rank *marsicanus* as a distinct ESU and, provisionally, a valid subspecies. Following a first call for action for the taxon, the need for a more vigorous approach to its conservation has been reiterated (Guacci et al. 2013; Gippoliti and Guacci 2017) given that the population size does not exceed 65 individuals including some 13 breeding females (Fig. 16.6) (Ciucci et al. 2015).

Although never openly debated, it is obvious that most bear experts in Europe believe that the first measure to ensure the long-term conservation of bears on the Apennine is restocking with a few individuals from the Balkans to allow 'genetic rescue'. This is in fact a continent-wide strategy, already utilized in the Alps and Pyrenees. Partly explaining the overt neglect of taxonomic issues – in a recent revision of 'Genetics and conservation of European brown bear *Ursus arctos*', the term



Fig. 16.6 An adult female Apennine bear. (Photo Antonio Macioce)

'taxonomy' is never used (Swenson et al. 2011). But if the unique characters of the skull of *marsicanus* are due to local adaptations as a result of directional selection instead of genetic drift (Colangelo et al. 2012), and evidence of inbreeding depression has never been observed, the picture that emerges is one of a lineage well adapted to a Mediterranean mountain habitat. A conservation strategy should, therefore, prioritize population expansion and not take the risk that the potentially unique gene pool is spoiled by introgression of genes from possibly 'less adapted' populations (outbreeding depression). The social organization of brown bears is characterized by female philopatry and male dispersal (Støen et al. 2005). Since male Apennine brown bears wander over several mountain systems of Central Italy, an important alternative conservation strategy would be to create new female breeding nuclei in other protected areas of the Apennine Mountains.

Given the taxonomic status of *marsicanus*, it has also been suggested that a bank of reproductive samples (semen, eggs) should be created - as has been planned in Spain for the Cantabrian brown bears (Anel et al. 2011; see also Saragusty et al. 2016) – and that if some bears have to be taken out of the wild population because they are 'problematic' (i.e. visiting villages to eat fruits and chicken), or are found orphaned in the wild, they should be included in an ex situ breeding program (Guacci et al. 2013). Benazzo et al. (2017) performed whole-genome sequencing of six Apennine bears comparing marsicanus with Iberian and Balkan Ursus arctos and divergence time was estimated at 3000-4000 years. They found evidence of two evolutionary processes with opposite outcomes: active maintenance of variation of specific families of genes and fixation by drift of several deleterious alleles. Their results thus support the view that, even in small populations, the random loss of variation does not affect all sites in the same way. Their work further contributes to the general debate about the relative role of drift and selection when the effective population size is very small. Interestingly, Benazzo et al. (2017)s conclusion is that 'On the other hand, the recognition of the Apennine bear as an Italian iconic endangered taxon, the possible risk of introducing aggressiveness genes and deteriorating the relatively peaceful human-bear coexistence in central Italy, and the current levels of variation at relevant immune and olfactory genes suggest avoiding genetic rescue' (Benazzo et al. 2017: 9595). This fully overlaps with Gippoliti's suggestion (2016) and strongly departs from the orthodoxy of bear management in Europe.

Although there is widespread concern for inbreeding depression, in the case of *marsicanus* there has been no national effort to conserve vouchers (skulls, skeletons, skins, etc.) of the many bears found dead due to human persecution. These materials should be critical to assess the health of the endemic Apennine bear. Hopefully, the slowly increasing evidence of the distinctiveness of *marsicanus* (see also Meloro et al. 2017) will lead to the development of a conservation plan that will effectively guide the recovery of the most endangered Italian mammals.

Incidentally, at least in the historic stronghold of the species, bears are considered by local inhabitants as a regional heritage, and in these regions, bears have never been aggressive towards humans and have a limited impact on human activities. In the end, we hope that social considerations too will help direct conservation strategy away from so-called genetic rescue.

16.7 Implications for Management and Conservation

There is no doubt that among the consequences of an overly simplified view of biodiversity, there is an oversimplified – and assuring – view of the environmental situation of the planet. The recognition of a given polytypic species with an enormous geographical distribution as a lower risk species completely overlooks the conservation status of several local populations/subspecies (Morrison III et al. 2009; Thakur et al. 2018) which, it is assumed, in case of continuing decline, could be 'restocked' with animals from other more healthy local populations (Frankham et al. 2012).

Promoting human-mediated genetic introgression, as supported by some biologists and philosophers (Sgrò et al. 2011; Rohwer and Marris 2016), is a step towards integrating and homogenizing conservation biology in an 'Anthropocene science' where we accommodate biological evolutionary history to the will of one species – Homo sapiens. Concern over the risks of homogenization of biological diversity of African bovids for commercial reasons has already been expressed by the IUCN/ SSC Antelope Specialist Group (IUCN SSC Antelope Specialist Group 2015). Translocation and genetic rescue is potentially an important technique that has been successfully utilized in several conservation projects, for example, with desert bighorn sheep (Hedrick and Wehausen 2014; Buchalski et al. 2016). But it can also be a waste of meagre conservation resources, not to mention of individual animals, in some instances such as the unsuccessful translocations of the 'woodland caribou' in Canada (Leech et al. 2017). In other words, before applying the 'magic bullet' of genetic rescue, look carefully at what is a species and what is not. What are the special adaptations of a declining population? Has 'genetic purging' occurred? And why has that population (or species) declined? Conservation is a very complex field. The decline of a population (or species) may have little or nothing to do with genetic impoverishment (Peer and Taborsky, 2005) and outbreeding depression may follow the 'top-up' of an endangered population by the introduction of fresh genes (Tallmon et al. 2004). An outdated and oversimplified taxonomy is one of the fundamental causes of a wrong-headed conservation strategy (Gippoliti et al. 2018a). Conservationists' motivations against adoption of an evolutionary species concept (Wiley 1978) seem to be due to a scarce knowledge of the 'species problem' outside the community of systematic biologists (Padial et al. 2010; Gutierrez and Helgen 2013; Raposo et al. 2017). We also reaffirm our opinion that the goal of conservation biology must be the maintenance of biodiversity biogeographical patterns that are as much as possible similar to those developed in the planet's history aside from human interventions.

Evolutionary thinking certainly justifies an increase in the number of mammal species that are recognized, including those that are threatened and those that are 'problematic' in their relationship with humans. But a clearer picture of existing biodiversity will, we hope, motivate the conservation community to direct resources through a transparent prioritization system. Once discovered, mammal lineages are particularly effective to serve as flagship and umbrella species for conservation of

otherwise neglected habitats. Further, it is urgent that – as was already evidenced by Caughley (1994) – a real integration between disciplines will be achieved. The belief that conservation problems stem automatically from small population sizes is a reductionist approach that may divert attention from true problems and the real solutions to species conservation. In the end, we think that such a finer approach to mammal taxonomy offers more opportunities for local communities' involvement in conservation and sustainable utilization is the only way we can hope to maintain a diverse and healthy planet.

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References

- Amori G, Angelici FM, Boitani L (1999) Mammals of Italy: a revised checklist of species and subspecies (Mammalia). Senckenberg Biol 79:271–286
- Anel L, Alvarez M, Anel E, Martinez-Pastor F, Martinez F, Chamorro C, de Paz P (2011) Evaluation of three different extenders for use in emergency salvaging of epididymal spermatozoa from a Cantabric brown bear. Reprod Domest Anim 46(1):e85–e90. https://doi. org/10.1111/j.1439-0531.2010.01646.x
- Angelici FM (ed) (2016) Problematic wildlife. A cross-disciplinary approach. Springer, Cham
- Angelone-Alasaad S, Biebach I, Peârez JM, Soriguer RC, Granados JE (2017) Molecular analyses reveal unexpected genetic structure in Iberian ibex populations. PLoS One 12(e0170827). https://doi.org/10.1371/journal.pone.0170827
- Alexander Ochoa, Stuart A. Wells, Gary West, Ma'en Al-Smadi, Sergio A. Redondo, Sydnee R. Sexton, Melanie Culver, (2016) Can captive populations function as sources of genetic variation for reintroductions into the wild? A case study of the Arabian oryx from the Phoenix Zoo and the Shaumari Wildlife Reserve, Jordan. Conservation Genetics 17(5):1145–1155
- Barlow A, James A, Cahill JA, Hartmann S et al (2018) Partial genomic survival of cave bears in living brown bears. Nat Ecol Evol. https://doi.org/10.1038/s41559-018-0654-8
- Benazzo A, Trucchi E, Cahill JA et al (2017) Survival and divergence in a small group: the extraordinary genomic history of the endangered Apennine brown bear stragglers. Proc Natl Acad Sci 114(45):E9589–E9597
- Bilton T, Mirol PM, Mascheretti S, Fredga K, Zima J, Searle JB (1998) Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. Proc R Soc Lond B 265:1219–1226
- Boitani L (ed) (1976) Reintroductions: techniques and ethics. Serie Atti e Studi n. 2. WWF Fondo Mondiale per la Natura, Rome
- Brooks M (2010) African rhino specialist group report. Pachyderm 48:8-15

- Buchalski MR, Sacks BN, Gille DA, Penedo MCT, Ernest HB, Morrison SA, Boyce WM (2016) Phylogeographic and population genetic structure of bighorn sheep (*Ovis canadensis*) in North American deserts. J Mammal 97:823–838
- Camerano L (1916) I caratteri del cranio, della colorazione e delle corna nella distinzione dei Camosci in specie e sottospecie. Riv Antropol 20:3–14
- Capasso Barbato L, Cerilli E, Petronio C (1993) Differenze morfologiche e morfometriche nei crani di *U. spelaeus* e *U. arctos*. Quaternario 6:67–76
- Carpaneto GM, Gippoliti S (1994) Primates of the Harenna Forest, Ethiopia. Primate Conserv 11:12–15
- Caughley G (1994) Directions in conservation biology. J Anim Ecol 63:215-244
- Cinková I, Policht R (2014) Contact calls of the Northern and Southern white rhinoceros allow for individual and species identification. PLoS One 9:e98475
- Ciucci P, Gervasi V, Boitani L, Boulanger J, Paetkau D, Prive R, Tosoni E (2015) Estimating abundance of the remnant Apennine brown bear population using multiple noninvasive genetic data sources. J Mammal 96:206–220
- Colangelo P, Loy A, Huber D, Gomerčić T, Vigna Taglianti A, Ciucci P (2012) Cranial distinctiveness in the Apennine brown bear: genetic drift or ecophenotypic adaptation? Biol J Linn Soc 107:15–26
- Conti S (1954) Morfologia comparata craniale ed encefalica degli orsi pleistocenici della Liguria. Correlazioni con alcune forme attuali (*U. arctos, U. marsicanus, U. horribilis*). Mem Mus Civ St Nat "G. Doria" Genova 1:1–66
- Cotterill FPD, Taylor PJ, Gippoliti S, Bishop JM, Groves CP (2014) Why one century of phenetics is enough: response to "are there really twice as many bovid species as we thought?". Syst Biol 63:819–832
- Cotterill FPD, Groves CP, Taylor PJ (2017) Taxonomy: refine rather than stabilize. Nature 547:162
- Culver M, Johnson WE, Pecon-Slattery J, O'Brien SJ (2000) Genomic ancestry of the American puma (*Puma concolor*). J Hered 91:186–197
- Curry-Lindahl K (1972) War and the white rhinos. Oryx 11:263-267
- de Beaux O (1930) Etica biologica. Tentativo di risveglio di una coscienza naturalistica. Temi, Trento
- de Beaux O (1932) Biological ethics. An attempt to arouse a naturalistic conscience. The Italian Mail and Tribune, Florence
- de Beaux O (1956) Posizione sistematica degli stambecchi e capre selvatiche viventi (*Capra* Linneo 1758) e loro distribuzione geografica. Atti Accad Sci Lett Genova 12:123–228
- Desalle R, Amato G (2017) Conservation genetics, precision conservation, and de-extinction. Hast Cent Rep 47:S18–S23
- Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Mol Ecol 16:463–475
- Ellerman JR, Morrison-Scott TCS (1951) Checklist of Palaearctic and Indian mammals 1758 to 1946. Trust of the British Museum, London
- Ferguson JWH (2002) On the use of genetic divergence for identifying species. Biol J Linn Soc 75:509–516
- Frankham R, Ballou JD, Dudash MR, Eldridge MDB, Fenster CB, Lacy RC, Mendelson JR III, Porton IJ, Ralls K, Ryder OA (2012) Implications of different species concepts for conservation biodiversity. Biol Conserv 153:25–31
- Garnett ST, Christidis L (2017) Taxonomy anarchy hampers conservation. Nature 546:25-27
- Geist V (2007) Defining subspecies, invalid taxonomic tools, and the fate of the woodland Caribou. Rangifer 17:25–28
- Gippoliti S (2006) Oscar de Beaux: a noteworthy Italian mammalogist and conservationist. Ital J Zool 73:285–289
- Gippoliti S (2011) Ex situ conservation programmes in European zoological gardens: can we afford to lose them? Biodivers Conserv 21:1359–1364
- Gippoliti S (2016) Questioning current practice in brown bear Ursus arctos conservation in Europe that undervalues taxonomy. Anim Biodivers Conserv 39:199–205

- Gippoliti S, Amori G (2002a) Mammal diversity and taxonomy in Italy: implications for conservation. J Nat Conserv 10:33–44
- Gippoliti S, Amori G (2002b) Anthropochorous mammal taxa and conservation lists. Conserv Biol 16:1162–1164
- Gippoliti S, Amori G (2007) Beyond 'threatened species' and 'reintroduction': establishing priorities for European rodents conservation and breeding programs in zoos. Int Zoo Yearb 41:194–202
- Gippoliti S, Battisti C (2017) More cool than tool: equivoques, conceptual traps and weaknesses of ecological networks in environmental planning and conservation. Land Use Policy 68:686–691
- Gippoliti S, Groves CP (2012) "Taxonomic inflation" in the historical context of mammalogy and conservation. Hystrix, It J Mamm 23:8–11
- Gippoliti S, Groves CP (2018) Overlooked mammal diversity and conservation priorities in Italy: impacts of taxonomic neglect on a biodiversity hotspot in Europe. Zootaxa 4434:511–528
- Gippoliti S, Guacci C (2017) Il più minacciato Mammifero italiano: l'orso marsicano. Un approccio interdisciplinare per la sua conservazione. Natura e Montagna 64:29–35
- Gippoliti S, Cotterill FPD, Zinner D, Groves CP (2018a) Impacts of taxonomic inertia for the conservation of African ungulate diversity: an overview. Biol Rev 93:115–130
- Gippoliti S, Cotterill FPD, Groves CP, Zinner D (2018b) Poor taxonomy and genetic rescue are possible co-agents of silent extinction and biogeographic homogenization among ungulate mammals. Biogeographia J Integr Biogeogr 33:41–54
- Goldstein PZ, DeSalle R, Amato G, Vogler AP (2000) Conservation genetics at the species boundary. Conserv Biol 14:120–131
- Groves CP (2001) Primate taxonomy. Smithsonian University Press, Washington
- Groves CP (2012) The nature of species: a rejoinder to Zachos et al. Mamm Biol 78:7-9
- Groves CP (2014) Primate taxonomy: inflation or real? Annu Rev Anthropol 43:27-36
- Groves CP, Grubb P (2011) Ungulate taxonomy. Johns Hopkins University Press, Baltimore
- Groves CP, Robovský J (2011) African rhinos and elephants: biodiversity and its preservation. Pachyderm 50:69–71
- Groves CP, Fernando P, Robovský J (2010) The sixth rhino: a taxonomic re-assessment of the critically endangered northern white rhinoceros. PLoS One 5:e9703. https://doi.org/10.1371/journal.pone.0009703
- Groves CP, Cotterill FPD, Gippoliti S, Robovský J, Roos C, Taylor PJ, Zinner D (2017) Species definitions and conservation: a review and case studies from African mammals. Conserv Genet 18:1247–1256
- Guacci C, Ferri M, Gippoliti S (2013) Un manifesto pro conservazione 'ex situ' dell'orso bruno marsicano Ursus arctos marsicanus Altobello, 1921. Biologia Ambientale 27(2):55–58
- Gutierrez EE, Helgen KM (2013) Mammalogy: outdated taxonomy blocks conservation. Nature 495:314
- Harley EH, de Waal M, Murray S, O'Ryan C (2016) Comparison of whole mitochondrial genome sequences of northern and southern white rhinoceroses (*Ceratotherium simum*): the conservation consequences of species definition. Conserv Genet 17:1285–1291
- Harris K, Nielsen R (2016) The genetic cost of Neanderthal introgression. Genetics 203:881-891
- Haus T, Akom E, Agwanda B, Hofreiter M, Roos C, Zinner D (2013) Mitochondrial diversity and distribution of African green monkeys (*Chlorocebus* Gray, 1870). Am J Primatol 75:350–360
- Hedrick PW, Fredrickson R (2010) Genetic rescue guidelines with examples from Mexican wolves and Florida panthers. Conserv Genet 11:615–626
- Hedrick PW, Wehausen JD (2014) Desert bighorn sheep: changes in genetic variation over time and the impact of merging populations. J Fish Wildl Manag 5:3–13
- Heller E (1913) The white rhinoceros. Smithsonian Miscell Collect 61(1):1-56
- Heller R, Frandsen P, Lorenzen ED, Siegismund HR (2013) Are there really twice as many bovid species as we thought? Syst Biol 62:490–493
- Hilmann-Smith K, Oyisenzoo ma M, Smith E (1986) A last chance to save the northern white rhino? Oryx 20:20–26

IUCN (1987) The IUCN position statement on translocation of living organisms. IUCN, Gland

- IUCN (1998) Guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. IUCN, Gland
- IUCN SSC Antelope Specialist Group (2015) IUCN SSC Antelope Specialist Group position statement on the intentional genetic manipulation of antelopes. Ver. 1.0
- IUCN/SSC (2013) Guidelines for reintroductions and other conservation translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp
- Kingdon J (1997) The kingdon field guide to African mammals. Collins, London
- Kuneš M, Bičík V (2002) Social and sexual behaviour in captive breeding groups of white rhinoceros. Acta Univ Palacki Olumuc Biol 39–40:81–99
- Katherine Ralls, Jonathan D. Ballou, Michele R. Dudash, Mark D. B. Eldridge, Charles B. Fenster, Robert C. Lacy, Paul Sunnucks, Richard Frankham, (2018) Call for a Paradigm Shift in the Genetic Management of Fragmented Populations. Conservation Letters 11 (2):e12412
- Leech H, Jelinski DE, DeGroot L, Kuzyk G (2017) The temporal niche and seasonal differences in predation risk to translocated and resident caribou (*Rangifer tarandus caribou*). Can J Zool 95:809–820
- Leopold A (1933) The conservation ethic. J Forestry 31:634-641
- Lindenmayer DB, Fisher J (2007) Tackling the habitat fragmentation panchreston. Trends Ecol Evol 22:127–132
- Marshall TC, Spalton JA (2000) Simultaneous inbreeding and outbreeding depression in reintroduced Arabian oryx. Anim Conserv 3:241–248
- Mayr E (1982) Of what use are subspecies? Auk 99:593–595
- Mekonnen A, Bekele A, Fashing PJ, Lernould JM, Atickem A, Stenseth NC (2012) Newly discovered Bale monkey populations in forest fragments in Southern Ethiopia: evidence of crop raiding, hybridization with grivets, and other conservation threats. Am J Primatol 74:423–432
- Mekonnen A, Fashing PJ, Bekele A et al (2017) Impacts of habitat loss and fragmentation on the activity budget, ranging ecology and habitat use of Bale monkeys (*Chlorocebus djamdjamen*sis) in the southern Ethiopian Highlands. Am J Primatol 9999:e22644. https://doi.org/10.1002/ ajp.22644
- Mekonnen A, Rueness EK, Stenseth NC, Fashing PJ, Bekele A, Hernandez-Aguilar RA, Missbach R, Tanja Haus T, Zinner D, Roos C (2018) Population genetic structure and evolutionary history of Bale monkeys (*Chlorocebus djamdjamensis*) in the southern Ethiopian Highlands. BMC Evol Biol 18:106
- Meloro C, Guidarelli G, Colangelo P, Ciucci P, Loy A (2017) Mandible size and shape in extant Ursidae (Carnivora, Mammalia): a tool for taxonomy and ecogeography. J Zool Syst Evol Res 55:269–287
- Morrison WR III, Lohr JL, Duchen P, Wilches R, Trujillo D, Mair M, Renner SS (2009) The impact of taxonomic change on conservation: does it kill, can it save, or is it just irrelevant? Biol Conserv 142:3201–3206
- Owen-Smith RN (2013) Ceratotherium simum white rhinoceros (grass rhinoceros, squarelipped rhinoceros). In J Kingdon and M Hoffmann (Eds), Mammals of Africa - Volume V (pp. 446–454). London, New Delhi, New York, Sydney: Bloomsbury
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Front Zool 7:16. https://doi.org/10.1186/1742-9994-7-16
- Peer K, Taborsky M (2005) Outbreeding depression, but no inbreeding depression in haplodiploid ambrosia beetles with regular sibling mating. Evolution 59:317–323
- Pocock RI (1932) The black and brown bears of Europe and Asia. J Bombay Nat Hist Soc 35:771-823
- Pocock RI (1935) The mammals collected in S.E. Arabia by Mr. Bertram Thomas and Mr. H. St. J. Philby. Ann Mag Nat Hist (10)15:441–467
- Raposo MA, Stopiglia R, Brito GRR, Bockmann FA, Kirwan GM, Gayon J, Dubois A (2017) What really hampers taxonomy and conservation? A riposte to Garnett and Christidis (2017). Zootaxa 4317(1):179–184

- Rohwer Y, Marris E (2016) Is there a prima facie duty to preserve genetic integrity in conservation biology? Ethics. Policy Environ 18(3):233–247
- Rojas M, (1992) The Species Problem and Conservation: What are We Protecting? Conservation Biology 6(2):170–178
- Rookmaaker K (2000) The alleged population reduction of the southern white rhinoceros (*Ceratotherium simum*) and the successful recovery. Säuget Mitt 45:55–70
- Saragusty J, Diecke S, Drukker M, Durrant B, Friedrich Ben-Nun I, Galli C, Göritz F, Hayashi K, Hermes R, Holtze S, Johnson S, Lazzari G, Loi P, Loring JF, Okita K, Renfree MB, Seet S, Voracek T, Stejskal J, Ryder OA, Hildebrandt TB (2016) Rewinding the process of mammalian extinction. Zoo Biol 35:280–292
- Schwarz E (1935) On ibex and wild goat. Ann Mag Nat Hist 16:433-437
- Seddon PJ, Soorae P (1999) Guidelines for subspecific substitutions in wildlife restoration projects. Conserv Biol 13:177–184
- Sexton JP, Hangartner SB, Hoffmann AA (2014) Genetic isolation by environment or distance: which pattern of gene flow is most common? Evolution 68:1–15
- Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change. Evol Appl 4:326–337
- Shackleton DM, Lovari S (1997) Classification adopted for the Caprinae survey pp. In: Shackleton DM (ed) Wild sheep and goats. Status survey and conservation action plan. IUCN/SSC Caprinae Specialist Group, Gland, pp 9–14
- Sipari E (1926) Relazione. Ente Autonomo del Parco Nazionale d'Abruzzo, Pescasseroli, 309 pp
- Støen O-G, Bellemain E, Sæbø S, Swenson J (2005) Kin-related spatial structure in brown bears Ursus arctos. Behav Ecol Sociobiol 59:191–197
- Stresemann E (1975) Ornithology. Harvard University Press, Cambridge, MA
- Swenson JE, Taberlet P, Bellemain E (2011) Genetics and conservation of European brown bear Ursus arctos. Mammal Rev 41:87–98
- Tallman DA, Luikart G, Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. Trends Ecol Evol 19:489–496
- Templeton A (1986) Coadaptation and outbreeding depression. In: Soulé (ed) Conservation biology. Sinauer Associates, Sunderland, pp 105–116
- Thakur M, Wullschleger Schättin E, McShea WJ (2018) Globally common, locally rare: revisiting disregarded genetic diversity for conservation planning of widespread species. Biodivers Conserv. https://doi.org/10.1007/s10531-018-1579-x
- Turcek FJ (1951) Effects of introductions on two game populations in Czechoslovakia. J Wildl Manag 15:113–114
- Turelli M, Barton NH, Coyne JA (2001) Theory and speciation. Trends Ecol Evol 19:490-496
- Vander Wal E, Garant D, Festa-Bianchet M, Pelletier F (2013) Evolutionary rescue in vertebrates: evidence, applications and uncertainty. Philos Trans R Soc B 368:20120090
- Vigna Taglianti A (2003) Ursus arctos note di sistematica. In: Boitani L, Lovari S, Vigna Taglianti A (eds) Fauna d'Italia. Mammalia III. Carnivora – Artiodactyla. Edizioni Calderini de il Sole 24 ORE, Bologna, pp 87–92
- Weeks AR, Sgrò CM, Young AG, Frankham R, Mitchell NJ, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, Breed MF, James EA, Hoffmann AA (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evol Appl 4:709–725
- Wheeler QD, Platnick NI (2000) The phylogenetic species concept (sensu Wheeler and Platnick).In: Wheeler QD, Meier R (eds) Species concepts and phylogenetic theory: a debate. Columbia University Press, New York, pp 55–69
- Wiley EO (1978) The evolutionary species concept reconsidered. Syst Zool 27:17-26
- Zachos FE, Clutton-Brock TH, Festa-Bianchet M, Lovari S, Macdonald DW, Schaller GB (2013) Taxonomy: species splitting puts conservation at risk. Nature 494:35