Questioning current practice in brown bear, *Ursus arctos*, conservation in Europe that undervalues taxonomy

S. Gippoliti

Gippoliti, S., 2016. Questioning current practice in brown bear, *Ursus arctos,* conservation in Europe that undervalues taxonomy. *Animal Biodiversity and Conservation*, 39.2: 199–205.

Abstract

Questioning current practice in brown bear, Ursus arctos, *conservation in Europe that undervalues taxonomy.*— The present paper highlights problems associated with the currently–accepted taxonomy of brown bear, *Ursus arctos,* and their consequences for conservation at the European level. The enormous morphological variability within *Ursus arctos* is not acknowledged in current taxonomy and conservation practice. Seven major clades are recognized in *Ursus arctos* by molecular researchers, and although Western Europe maintains most of the populations belonging to the relict Clade 1 brown bear lineage, no reference to this is made in current conservation policy. Furthermore, the tiny population of Apennine brown bears, characterized by unique skull morphology, is not even recognized as a distinct Evolutionari Significant Unit (ESU) by current European legislation, nor is it included in the IUCN Red List. This may have serious consequences as brown bear conservation in Western Europe has been mainly based on restocking and reintroduction programs.

Key words: Ursus arctos marsicanus, Italy, Species concepts, Conservation, Semen banking, ESU

Resumen

Cuestionamiento de la actual estrategia de conservación del oso pardo, Ursus arctos, *en Europa, que infravalora la taxonomía.*— En este trabajo se ponen de relieve los problemas relacionados con la taxonomía actualmente aceptada del oso pardo, *Ursus arctos*, y sus consecuencias para la conservación en el ámbito europeo. En la actualidad, ni la taxonomía ni las prácticas de conservación reconocen la enorme variabilidad morfológica existente dentro de la especie *Ursus arctos*. Los investigadores moleculares reconocen la existencia de siete clados principales en *Ursus arctos* y, a pesar de que en Europa occidental la mayoría de las poblaciones pertenecen al primitivo Clado 1 del linaje de oso pardo, en las políticas vigentes de conservación no se hace referencia a ello. Además, la diminuta población de osos pardos de los Apeninos, caracterizada por una morfología craneal particular, ni siquiera es reconocida como una unidad evolutiva significativa (UES) por la legislación europea vigente ni tampoco está incluida en la Lista Roja de la UICN. Ello puede tener graves consecuencias, puesto que la conservación del oso pardo en Europa occidental se ha basado principalmente en programas de repoblación y reintroducción.

Palabras clave: Ursus arctos marsicanus, Italia, Conceptos de especie, Conservación, Banco de semen, UES

Received: 23 I 16; Conditional acceptance: 18 III 16; Final acceptance: 21 IV 16

Spartaco Gippoliti, Società Italiana per la Storia della Fauna 'G. Altobello', Viale Liegi 48, 00198 Roma (Italy).

E-mail: spartacolobus@hotmail.com

Introduction

More than 150 years since the publication of Darwin's 'Origin of Species' (Darwin, 1859), philosophical and biological issues regarding speciation and species boundaries are still debated (Hey, 2006; Naomi, 2011). In effect, conservation assessments usually include a review of what is deemed 'currently accepted taxonomy', with little understanding that taxonomy is in fact a specialist discipline, and that 'currently accepted' carries little or no scientific weight if not supported by updated taxonomic revisions (Gutierrez & Helgen, 2013). The conservation of biodiversity ultimately depends upon the work of taxonomists (McNeely, 2002). While it is clear that our knowledge is still limited for most tropical regions, it is often overlooked that, even in Europe, new assessments of the taxonomy of particular groups often lead to species descriptions (Fontaine et al., 2012).

Occasional conflicts between mammal taxonomists and conservationists have been observed in recent years (*i.e.*, Isaac et al., 2004; Groves & Robovský, 2011; Shetty & Vidya, 2011; Cotterill et al., 2014). The case of the brown bear, *Ursus arctos* Linnaeus, 1758, represents a notable example of the neglect of taxonomic issues in the current approaches for the conservation of large mammals.

It is well established that the polar bear, *Ursus maritimus*, Phipps, 1774 is closely allied to *Ursus arctos* Linnaeus, 1758. However, patterns of mitochondrial DNA have failed to confirm the reciprocal monophyly of the two taxa (Talbot & Shields, 1996).

The species status of the polar bear has never been seriously questioned, and new data with other molecular markers appear to have reestablished the 'true relationship' between the two species (Cronin et al., 2013). Yet the hypothesis that polar bears originated from an island brown bear population, so that these brown bears are phylogenetically closer to polar bears than, for example, Gobi Desert brown bears, seems perfectly credible and merits further examination.

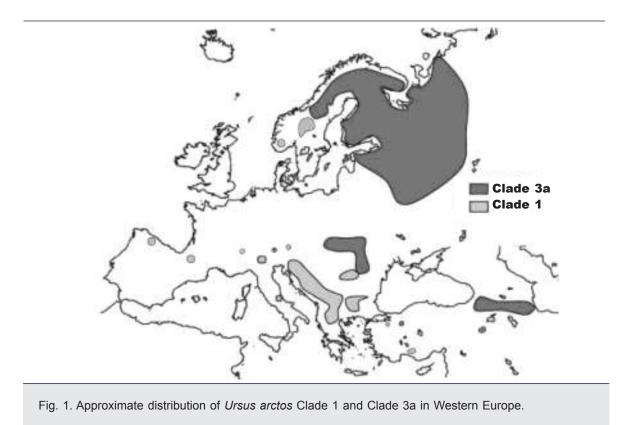
It is of interest that no studies to date have yet used molecular data to provide an alternative to the now classic 'one species' approach to *Ursus arctos* taxonomy, despite evidence of several deeply divergent mtDNA monophyletic clades within '*arctos*' (Galbreath et al., 2007).

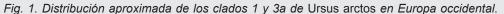
Furthermore, current awareness of the historical occurrence of hybridization and introgression between polar and brown bears (Edwards et al., 2011; Bidon et al., 2014) seems to support the need to adopt a different approach to species delimitation in the *U. arctos* complex away from the interbreeding criteria adopted as the fundamental pillar by the biological species concept. In the present paper we contend that the time is ripe for a taxonomic revision of the whole *U. arctos* complex, adopting an integrative coherent approach.

In the meantime, we here review available evidence with the aim of integrating the present conservation strategy for brown bear conservation within the European Union.

What are the consequences for brown bear conservation?

The taxonomic history of brown bears has been complicated owing to the great deal of phenotypic variation found both locally and regionally (Kitchener, 2010). Most modern researchers therefore simply choose to ignore the issue. Despite the availability of a wealth of genetic data in recent years (Swenson et al., 2011), its taxonomic significance has not been investigated (Kitchener, 2010; see below), or only rarely (Galbreath et al., 2007). In the specific IUCN/SSC Action Plan, the presence of possible taxonomically divergent populations in such a widespread species is simply overlooked (Servheen et al., 1998) with the consequence that the whole species is not considered as threatened (Least Concern; McLellan et al., 2008). Such treatment is prone to type 2 and 3 taxonomic errors (Cotterill et al., 2014), and one or more cryptic lineages may be at unnoticed risk of becoming extinct (Calvignac et al., 2009). In Europe, the species is included in Annex II of the Habitat Directive, but no attention is given to conservation below the species level. A major finding of genetic research, never fully translated into taxonomy and conservation strategy, is that the U. arctos complex can be separated into seven major geographically structured mitochondrial DNA clades and a small number of subclades (Hirata et al., 2013; Ashrafzadeh et al., 2016). Current EU bear conservation strategies (*i.e.*, Boitani et al., 2015) seem to completely overlook that some of the Western European populations belong to the relict mtDNA lineage Clade 1, mainly restricted to the Iberian, Italian, Balkan and Southern Scandinavian Peninsulas (Davison et al., 2011; Hirata et al., 2013; fig. 1), and recently discovered in Western Turkey (fig. 1; Çilingir et al., 2015). The value of recognized clades as conservation management units has been challenged in Europe by Valdiosera et al. (2007), who found Clade 3 mtDNA in ancient bear samples from within the current Clade 1 range in Northern Spain. These results have been interpreted as suggesting that present brown bear lineages are more the result of range fragmentation by humans than of evolutionary significant units (Valdiosera et al., 2008). The issue deserves further study as it is highly probable that with changing environmental conditions (*i.e.*, glacials), Europe was colonized by mammal lineages of Eastern origin that retreated during interglacial periods, while Mediterranean lineages survived in southern refugia. For instance, during the Late Glacial, both Lynx lynx (Linnaeus, 1758) and L. pardinus (Temminck, 1827) occurred on the Iberian peninsula (Sommer & Benecke, 2006) and even in the northern Italian peninsula (Rodríguez-Varela et al., 2015), confirming their evolutionary species status. The size of the populations belonging to U. arctos Clade 1, wholly restricted to Europe, is difficult to estimate from available data because some of the 'populations' considered by EU experts (Scandinavian, Carpathian) are centered in the contact area where Clade 1 meets the worldwide Clade 3 (Zachos et al., 2008; Xenikoudarkis et al., 2015). It seems that so far no study has addressed





the question of whether the two clades are also distinguishable morphologically, as has been attempted elsewhere (*e.g.*, Baryshnikov et al., 2004).

Bear conservation in the EU and the overlooked demise of the Apennine bear

Large carnivore populations, including brown bears, have recently been described as flourishing in EU states (Chapron et al., 2014). Attempts have been made to reestablish almost extinct brown bear populations (Alps, Pyrenees) through the translocation of bears from viable populations elsewhere. As in the rest of the world, no intraspecific taxonomic units have been accepted by bear experts in Europe (Swenson et al., 2000; Swenson et al., 2011). Accordingly, it has been emphasized that the Croatian bear population would appear to satisfy all criteria to serve as a source population for future reintroduction projects in Western Europe (Kocijan et al., 2011). This approach to brown bear conservation in Europe has been challenged with specific reference to the small, isolated Apennine brown bear population whose only breeding nucleus is found in the National Park of Abruzzo, Lazio and Molise, in Italy (Guacci et al., 2013). The original description of U. arctos marsicanus Altobello, 1921, based on limited materials, was rightly dismissed by Pocock (1932) who was aware of the considerable morphological variability found in *U. arctos*. Yet this view has been shared without any further study of new materials throughout the 20th Century, a period of taxonomic inertia for European mammalogy (Gippoliti & Groves, 2013).

According to early genetic studies (Randi et al., 1994; Taberlet & Buvet, 1994), this population, together with the Balkan populations, is considered to belong to the western brown bear clade 1b and shows negligible differentiation. But more recently, both Randi (2003) and Lorenzini et al. (2004) have indicated that differences in mitochondrial DNA and microsatellites suggest a distinct management unit. Furthermore, evidence is mounting that Apennine brown bears have a considerable phenotypic distinctiveness ---specifically regarding the skull (Conti, 1954; Loy et al., 2008; Colangelo et al., 2012), to the extent that all these authors accepted U. arctos marsicanus as a valid taxon. Capasso Barbato et al. (1993), while discussing the cranial characters of extant U. arctos populations and U spelaeus Rosenmuller, 1784, confirmed that U. arctos marsicanus share some peculiarities with U. spelaeus, as previously evidenced by Conti (1954). This unusual situation can hardly be explained simply as the result of 'genetic drift' due to isolation from the main continental bear population in the last 400-700 years (cfr. Ministry of the Environment, 2011; Colangelo et al., 2012). The stability of a suture zone in Scandinavia in the last 150 years, with the two clades only a few kilometers apart (Xenikoudarkis et al., 2015), demands that historical connectivity between the Apennine and Alps populations be verified and not merely automatically inferred. It seems reasonable at this stage to consider the Apennine brown bear as a southern endemic survivor, like the Apennine chamois *Rupicapra ornata* Neumann, 1899 (Vigna–Taglianti, 2003).

At this point, one would surely have expected a revision of conservation policies both nationally and at the EU level. Nothing of the kind happened. Guacci et al. (2013) called for a more pressing conservation strategy for this endemic Italian taxon, including, if necessary, captive breeding and a bank of biomaterials —an aspect that is not considered in the National Action Plan (Ministry of the Environment, 2011), but is pursued elsewhere through semen collection from live individuals or post-mortem recovery of epididymal spermatozoa (Fickel et al., 2007; Anel et al., 2011). At present, it seems that conservation authorities and bear researchers continue to emphasize ecological connectivity between Apennine protected areas to create new breeding nuclei and reduction of human-induced mortality. If such an approach does not lead to positive results (for instance, due to female brown bear philopatry and thus dispersal avoidance outside their natal range), no alternative strategy seems to exist ---or, better, the only available way to maintain genetic variability and increase range size in the future would be to bolster this population with individuals from the closest viable wild population, as done elsewhere (Chapron et al., 2009). Even if this intervention vigorously followed the IUCN Guidelines for reintroductions and other conservation translocations, given the unique status of U. arctos marsicanus among brown bears, it is clear that no candidate population exists. In 2008 it was stated that: 'The reconsideration and acceptance of the Apennine population as a distinct taxon will have a strong effect on any action to be undertaken for the conservation of the species in Italy' (Loy et al., 2008). As Randi (2003) also stressed: 'there should be distinct conservation managements for the Alpine and Apennine brown bear populations, and Apennine brown bears should be managed as an evolutionary significant unit (ESU)' (Loy et al., 2008). It should be emphasized that although the small population size (about 50 individuals, including circa 13 breeding females; cfr. Ciucci et al., 2015) is obviously a cause for concern, so far, no obvious effects of inbreeding have been reported. Although captive-breeding is not generally considered a viable option for brown bear conservation (Huber, 2010), Guacci et al. (2013) stressed that release of orphan bears is a common practice in several parts of the world (cfr. Beecham et al., 2015). Thus, if it is necessary to save a threatened taxon, captive-bred cubs could be released adopting a similar approach. Although starting a captive breeding program is a considerable risk with this current population status, since the 1990s, four Apennine brown bears have been kept in captivity (roughly 10% of the wild adult population). No serious attempts have been made to breed these bears, however, because it is assumed that captive-bred bears would not be successfully released back to the wild. Apart from captive breeding, however, it is time to recognize that our goal in Central Italy is the conservation of *U. arctos marsicanus* —an endemic taxon— and not simply that of the Apennine brown bear population.

Moving ahead in the conservation of brown bear diversity

Only today are we beginning to appreciate how decades of game management and wildlife translocations, without adequate backup from zoology and especially from taxonomy, has led us to overlook the fate of native Italian endemic taxa of ungulates (such as wild boars, Sus scrofa majori De Beaux & Festa, 1927 and roe deer, Capreolus capreolus italicus Festa, 1925), to the point where their re-establishment is near impossible given the presence of introduced alien stocks (Gippoliti & Amori, 2002; Champagnon et al., 2012). Even with carnivores such as the Eurasian otter Lutra lutra, awareness of the presence of a distinctive ESU in southern Italy (Panzacchi et al., 2010) came just in time to block some reintroduction programs. The Southern European Peninsulas of Iberia, Italy and the Balkans are known today to maintain a number of endemic lineages that make them a conservation priority; these lineages include the most threatened cat species in the world, Lynx pardina, considered a subspecies of Lynx lynx until 20 years ago (Beltrán et al., 1996).

The European Union needs to re–evaluate its conservation policy. A premium must be assigned to the conservation of populations that have not been altered by human–assisted genetic introgression. Only in this way can we effectively increase awareness of European biodiversity heritage.

As regards the conservation of brown bear in Europe, it has been suggested that an integrative approach to taxonomic research should be adopted. In the meantime, no measure should be proposed to encourage gene flow in the contact zone between Clade 1 and Clade 3. In the case of relict Clade 1 populations, such as the Apennine marsicanus, immediate action, as recognized by current conservation plans (Boitani et al., 2015; Ministry of the Environment, 2011), must be integrated by a long-term approach to secure genetic materials for future use, as has been done for the Cantabrian population (Nicolas et al., 2010). The precautionary principle and available scientific evidence demand that we manage U. arctos marsicanus as a distinct ESU. As such, future re-stocking with individuals from other populations is clearly not recommended.

Augmentation of the Apennine bear population has never been officially proposed. Any such project would raise serious safety concerns among local communities, who have never reported incidents with Apennine bears. Furthermore, such a project would lead to a hybrid swarm or substitution of a unique brown bear taxon before we fully understand the origin, history and significance of *U. arctos marsicanus*.

Acknowledgments

D. Fontaneto, C. P. Groves, B. Krystufek, G. Milana and D. Zinner read earlier drafts and made suggestions that greatly improved the final text. An anonymous referee and Susana Gonzalez provided useful comments and suggestions regarding an early version of the manuscript.

References

- 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 epididiymal spermatozoa from a Cantabric brown bear. *Reproduction Domestic Animals*, 46(1): e85–90. Doi: 10.1111/j.1439– 0531.2010.01646.x.
- Ashrafzadeh, M. R., Kaboli, M. & Naghavi, M. R., 2016. Mitochondrial DNA analysis of Iranian brown bears (*Ursus arctos*) reveals new philogeographic lineage. *Mammalian Biology*, 81: 1–9.
- Baryshnikov, G. F., Mano, T. & Masuda, R., 2004. Taxonomic differentiation of Ursus arctos (Carnivora, Ursidae) from south of Okhotsk Sea Islands on the basis of morphometrical analysis of skull and teeth. Russian Journal of Theriology, 3: 77–88.
- Beecham, J. J., De Gabriel Hernando, M., Karamanlidis, A. A., Beausoleil, R. A., Burguess, K., Jeong, D.–H., Binks, M., Bereczky, L., Ashraf, N. V. K., Skripova, K., Rhodin, L., Auger, J. & Lee, B.–K., 2015. Management implications for releasing orphaned, captive–reared bears back to the wild. *Journal of Wildlife Management*, 79: 1327–1336.
- Beltrán, J. F., Rice, J. E. & Honeycutt, R. L., 1996. Taxonomic status of the Iberian lynx. *Nature*, 379: 407–408.
- Bidon, T., Janke, A., Fain, S. R., Eiken, H. G., Hagen, S. B., Saarma, U., Hallström, B. M., Lecomte, N. & Hailer, F., 2014. Brown and polar bear Y chromosomes revealextensive male–biased gene flow within brother lineages. *Molecular Biology and Evolution*, 31: 1353–1363.
- Boitani, L., Alvarez, F., Anders, O., Andren, H., Avanzinelli, E., Balys, V., Blanco, J., Breitenmoser, C. U., Chapron, G., Ciucci, P., Dutsov, A., Groff, C., Huber, D., Ionescu, O., Knauer, F., Kojola, I., Kubala, J., Kutal, M., Linnell, J., Majic, A., Mannil, P., Manz, R., Marucco, F., Melovski, D., Molinari, A., Norberg, H., Nowak, S., Ozolins, J., Palazon, S., Potocnik, H., Quenette, P.–Y., Reinhardt, I., Rigg, R., Selva, N., Sergiel, A., Shkvyria, M., Swenson, J., Trajce, A., Von Arx, M., Wolfl, M., Wotschikowsky, U. & Zlatanova, D., 2015. *Key actions for Large Carnivore populations in Europe*. Institute of Applied Ecology (Rome, Italy). Report to DG Environment, European Commission, Bruxelles. Contract no. 07.0307/2013/654446/SER/B3.
- Calvignac, S., Hughes, S. & Hänni, C., 2009. Genetic diversity of endangered brown bear (*Ursus arctos*) populations at the crossroads of Europe, Asia and Africa. *Diversity and Distribution*, 15: 742–750.

- Capasso Barbato, L., Cerilli E. & Petronio, C., 1993. Differenze morfologiche e morfometriche nei crani di *U. spelaeus* e *U. arctos. II Quaternario*, 6: 67–76.
- Champagnon, J., Eimberg, J., Guillemain, M., Gauthier–Clerc, M. & Lebreton, J.–M., 2012. Conspecifics can be aliens too: A review of effects of restocking practices in vertebrates. *Journal for Nature Conservation*, 20: 231–241.
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K, Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., W. Mysłajek, R. W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J. E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L., 2014. Recovering of large carnivores in Europe's modern humandominated landscapes. Science, 346: 1517-1519
- Chapron, G., Wielgus, R., Quenette, P.–Y. & Camarra, J.–J., 2009. Diagnosing Mechanisms of Decline and Planning for Recovery of an Endangered Brown Bear (*Ursus arctos*) Population. *PLoS ONE*, 4(10): e7568. Doi:10.1371/journal.pone.0007568.
- Çilingir, F. G., Pekşen, C. A., Ambarli, H., Beerli, P. & Bilgin, C. C., 2015. Exceptional maternal lineage diversity in brown bears (*Ursus arctos*) from Turkey. *Zoological Journal of the Linnean Society*. Doi: 10.1111/zoj.12322.
- 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. *Journal of Mammalogy*, 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? *Biological Journal of the Linnean Society*, 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). Memorie Museo Civico di Storia Naturale "G. Doria" Genova, 1: 1–66.
- Cotterill, F. P. D., Taylor, P. J., Gippoliti, S., Bishop, J. M. & Groves, C. P., 2014. Why one century of phenetics is enough: response to 'Are there really twice as many bovid species as we thought?'. *Systematic Biology*, 63: 819–832.
- Cronin, M. A., McDonough, M. M., Hurynh, H. M. & Baker, R. J., 2013. Genetic relationships of North American bears (*Ursus*) inferred from amplified

fragment length polymorphisms and mitochondrial DNA sequences. *Canadian Journal of Zoology*, 91: 626–634.

- Darwin, C., 1859. On the origin of species by means of natural selection. Murray, London.
- Davison, J., Ho, S. Y. W., Bray S. C., Korsten, M., Tammeleht, E., Hindrikson, M., Østbye, K., Østbye, E., Lauritzen, S.–E., Austin, J., Cooper, A. & Saarma, U., 2011. Late–Quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. *Quaternary Science Reviews*, 30: 418–430.
- Edwards, C. J., Suchard, M. A., Lemey, P., Welch, J. J., Barnes, I., Fulton, T. L., Barnett, R., O'Connell, T. C., Coxon, P., Monaghan, N., Valdiosera, C. E., Lorenzen, E. D., Willerslev, E., Baryshnikov, G. F., Rambaut, A., Thomas, M. G., Bradley, D. G. & Shapiro, B., 2011. Ancient hybridization and an Irish origin for the modern polar bear matriline. *Current Biology*, 21: 1251–1258.
- Fickel, J., Wagener, A. & Ludwig, A., 2007. Semen cryopreservation and the conservation of endangered species. *European Journal of Wildlife Research*, 53: 81–89.
- Fontaine, B., van Achterberg, K., Alonso-Zarazaga, M. A., Araujo, R., Asche, M., Aspöck, H., Aspöck, U., Audisio, P., Aukema, B., Bailly, N., Balsamo, M., Bank, R. A., Belfiore, C., Bogdanowicz, W., Boxshall, G., Burckhardt, D., Chylarecki, P., Deharveng, L., Dubois, A., Enghoff, H., Fochetti, R., Fontaine, C., Gargominy, O., Gomez Lopez, M. S., Goujet, D., Harvey, M. S., Heller, K.-G., van Helsdingen, P., Hoch, H., de De Jong, Y., Karsholt, O., Los, W., Magowski, W., Massard, J. A., McInnes, S. J., Mendes, L. F., Mey, E., Michelsen, V., Minelli, A., Nieto Nafria, J. M., van Nieukerken, E. J., Pape, T., De Prins, W., Ramos, M., Ricci, C., Roselaar, C., Rota, E., Segers, H., Timm, T., van Tol, J. & Bouchet, P., 2012. New Species in the Old World: Europe as a Frontier in Biodiversity Exploration, a Test Bed for 21st Century Taxonomy. PLoS ONE, 7(5): e36881. Doi: 10.1371/journal.pone.0036881.
- Galbreath, G. J., Groves, C. P. & Waits, L. P., 2007. Genetic resolution of composition and phylogenetic placement of the isabelline bear. *Ursus*, 18: 129–131.
- Gippoliti, S. & Amori, G., 2002. Mammal diversity and taxonomy in Italy: implications for conservation. *Journal for Nature Conservation*: 10, 133–143.
- Gippoliti, S. & Groves, C. P., 2013. 'Taxonomic inflation' in the historical context of mammalogy and conservation. *Hystrix Italian Journal of Mammalogy*, 23: 6–9. Doi: 10.4404/hystrix–23.2–8685.
- Groves, C. P. & Robovský, J., 2011. African rhinos and elephants: biodiversity and its preservation. *Pachyderm*, 50: 69–71.
- 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 (in Italian).
- Gutierrez, E. E. & Helgen, K. M., 2013. Mammalogy: outdated taxonomy blocks conservation. *Nature*, 495: 314.

- Hey, J., 2006. On the failure of modern species concepts. *Trends in Ecology and Evolution*, 21: 447–450.
- Hirata, D., Mano, T., Abramov, A. V., Baryshnikov, G. F., Kosintsev, P. A., Vorobiev, A. A., Raicher, E. G., Tsuinda, H.,Kaneko, Y., Murata T., Fukui, D. & Masuda, R., 2013. Molecular phylogeography of the brown bear (*Ursus arctos*) in northeastern Asia based on analyses of complete mitochondrial DNA sequences. *Molecular Biology and Evolution*, 30: 1644–1652.
- Huber, D., 2010. Rehabilitation and reintroduction of captive–reared bears: feasibility and methodology for European brown bears *Ursus arctos*. *International Zoo Yearbook*, 44: 47–54.
- Isaac, N. J. B., Mallet, J. & Mace, G. M., 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology and Evolution*, 19: 464–469.
- Kitchener, A. C., 2010. Taxonomic issues in bears: impacts on conservation in zoos and the wild, and gaps in current knowledge. *International Zoo Yearbook*, 44: 33–46.
- Kocijan, I., Ćetković, H., Kusak, J., Gomerćić, T. & Huber, Đ., 2011. Genetic diversity of Dinaric brown bears (*Ursus arctos*) in Croatia with implications for bear conservation in Europe. *Mammalian Biology*, 76: 615–621.
- Lorenzini, R., Posillico, M., Lovari, S. & Petrella, A., 2004. Non–invasive genotyping of the endangered Apennine brown bear: a case study not to let one's hair down. *Animal Conservation*, 7: 199–209.
- Loy, A., Genov, P., Galfo, M., Jacobone, M. G. & Vigna Taglianti, A., 2008. Cranial morphometrics of the Apennine brown bear (*Ursus arctos marsicanus*) and preliminary notes on the relationships with other southern populations. *Italian Journal of Zoology*, 75: 67–75.
- McLellan, B. N., Servheen, C. & Huber, D., 2008. Ursus arctos. The IUCN Red List of Threatened Species. Version 2014.3. [Accessed on 28 November 2014].
- McNeely, J. A., 2002. The role of taxonomy in conserving biodiversity. *Journal for Nature Conservation*, 10: 145–153.
- Ministry of the Environment, 2011. *Piano d'azione nazionale per la tutela dell'orso marsicano – PA-TOM*. Ministry of the Environment, Rome: 1–54 (in Italian).
- Naomi, S. I., 2011. On the integrated frameworks of species concepts: Mayden's hierarchy of species concepts and de Queiroz's unified concept of species. *Journal Zoological Systematics and Evolutionary Research*, 49(3): 177–184.
- Nicolas, M., Alvarez, M., Gomes–Alves, S., Mata– Campuzano, M., Borragán, S., Martinez–Pastor, F., de Paz, P. & Anel, L., 2010. Effects on brown bear (*Ursus arctos*) spermatozoa freezability of different extender and dilution ratios used for prefreezing centrifugation. *Theriogenology*, 77: 1119–1128.
- Panzacchi, M., Genovesi, P. & Loy, A., 2010. *Piano d'Azione nazionale per la conservazione della lontra* (Lutra lutra). Ministry of the Environment

and ISPRA, Rome. (In Italian).

- Pocock, R. I., 1932. The black and brown bears of Europe and Asia. *Journal Bombay Natural History Society*, 35: 771–823.
- Randi, E., 2003. Conservation genetics of carnivores in Italy. Compte Rendus Biologies, 326: S54–S60.
- Randi, E., Gentile, L., Boscagli, G., Huber, D. & Roth, H. U., 1994. Mitochondrial DNA sequence divergence among some west brown bear (*Ursus arctos* L.) populations. Lessons for conservation. *Heredity*, 73: 480–489.
- Rodríguez–Varela, R., Tagliacozzo, A., Ureña, I., García, N., Crégut–Bonnoure, E., Mannino, M. A., Arsuaga, J. L. & Valdiosera, C., 2015. Ancient DNA evidence of Iberian lynx palaeoendemism. *Quaternary Science Reviews*, 112: 172–180.
- Servheen, C., Herrero, S. & Peyton, B. (Eds.), 1998. *Bears: status survey and conservation action plan.* IUCN, Gland, Switzerland.
- Shetty, N. R. & Vidya, T. N. C., 2011. To split or not to split: the case of the African elephant. *Current Science*, 100(6): 810–812.
- Sommer, R. S. & Benecke, N., 2006. Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. *Journal of Zoology*, 269: 7–19.
- Swenson, J. E., Gerstl, N., Dahle, B. & Zedrosser, A., 2000. Action Plan for the conservation of the brown bear (Ursus arctos). Coucil of Europe, Strasbourg, France.
- Swenson, J. E., Taberlet, P. & Bellemain, E., 2011 Genetics and conservation of European brown bears Ursus arctos. Mammal Review, 41: 87–98.

Talbot, S. L. & Shields, G. F., 1996. Phylogeography

of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecolar Phylogeny and Evolution*, 5: 477–494.

- Xenikoudarkis, G., Ersmark, E., Tison, J.–L., Waits, L., Kindberg, J., Swenson, J. E. & Dalén, L., 2015. Consequences of a demographic bottleneck on genetic structure and variation in the Scandinavian brown bear. *Molecular Ecology*. Doi: 10.1111/ mec.13239.
- Valdiosera, C. E., Garcıa, N., Anderung, C., Dalén L., Crégut–Bonnoure, E., Kahlke, R. D., Stiller, M., Brandström, M., Thomas, M. G., Arsuaga, J. L., Götherström, A. & Barnes, I., 2007. Staying out in the cold: glacial refugia and mitochondrial DNA phylogeography in ancient European brown bears. *Molecular Ecology*, 16: 5140–5148.
- Valdiosera, C. E., García–Garitagoitia, J. L., Garcia, N., Doadrio, I., Thomas, M. G., Hänni, C., Arsuaga, J.–L., Barnes, I., Hofreiter, M., Orlando, L. & Götherström, A., 2008. Surprising migration and population size dynamics in ancient Iberian brown bears (*Ursus arctos*). *Proceedings of the National Academy of Sciences of the United States* of America, 105: 5123–5128.
- Vigna Taglianti, A., 2003. Ursus arctos. Note di sistematica. In: *Fauna d'Italia. Mammalia III. Carnivora–Artiodactyla*: 87–92 (L. Boitani, S. Lovari & A. Vigna Taglianti, Eds.). Edizioni Calderini de II Sole 24 ore, Bologna.
- Zachos, E. F., Otto, M., Unici, R., Lorenzini, R. & Hartl, G., 2008. Evidence of a phylogeographic break in the Romanian brown bear (*Ursus arctos*) population from the Carpathians. *Mammalian Biology*, 73: 93–101.