

WILDLIFE BIOLOGY

Research

Past, present and future of chamois science

L. Corlatti, L. Iacolina, T. Safner, M. Apollonio, E. Buzan, F. Ferretti, S. E. Hammer, J. Herrero, L. Rossi, E. Serrano, M. C. Arnal, F. Brivio, R. Chirichella, A. Cotza, B. Crestanello, J. Espunyes, D. Fernández de Luco, S. Friedrich, D. Gačić, L. Grassi, S. Grignolio, H. C. Hauffe, K. Kavčić, A. Kinser, F. Lioce, A. Malagnino, C. Miller, W. Peters, B. Pokorny, R. Reiner, A. Rezić, S. Stipoljev, T. Tešija, Y. Yankov, T. Zwijacz-Kozica and N. Šprem

L. Corlatti (<https://orcid.org/0000-0002-2706-3875>) ✉ (luca.corlatti@wildlife.uni-freiburg.de), Chair of Wildlife Ecology and Management, Univ. of Freiburg, Freiburg, Germany and Stelvio National Park, Bormio, Italy. – L. Iacolina (<https://orcid.org/0000-0001-5504-6549>) and E. Buzan (<https://orcid.org/0000-0003-0714-5301>), Faculty of Mathematics, Natural Sciences and Information Technologies, Univ. of Primorska, Koper, Slovenia. LI also at: Aalborg Univ., Dept of Chemistry and Biosciences, Aalborg, Denmark. – T. Safner (<https://orcid.org/0000-0001-8645-5273>) and T. Tešija (<https://orcid.org/0000-0002-5422-1306>), Faculty of Agriculture, Dept of Plant Breeding, Genetics and Biometrics, Univ. of Zagreb, Zagreb, Croatia. TS also at: Centre of Excellence for Biodiversity and Molecular Plant Breeding (CoE CroP-BioDiv), Zagreb, Croatia. – M. Apollonio (<https://orcid.org/0000-0002-8953-9138>), F. Brivio (<https://orcid.org/0000-0002-1449-8335>) and R. Chirichella (<https://orcid.org/0000-0001-6734-5319>), Dept of Veterinary Medicine, Univ. of Sassari, Sassari, Italy. – EB and B. Pokorny (<https://orcid.org/0000-0002-2981-5516>), Faculty of Environmental Protection, Velenje, Slovenia. – F. Ferretti (<https://orcid.org/0000-0002-0414-1615>) and A. Cotza (<https://orcid.org/0000-0002-6092-9079>), Research Unit of Behavioural Ecology, Ethology and Wildlife Management, Dept of Life Sciences, Univ. of Siena, Siena, Italy. – S. E. Hammer (<https://orcid.org/0000-0003-1475-3938>), Inst. of Immunology, Dept of Pathobiology, Univ. of Veterinary Medicine, Vienna, Austria. – J. Herrero, Dept of Agrarian and Environmental Science, Univ. of Zaragoza, Huesca, Spain. – L. Rossi, Dept of Veterinary Sciences, Univ. of Turin, Grugliasco (TO), Italy. – E. Serrano (<https://orcid.org/0000-0002-9799-9804>), Wildlife Ecology & Health Group (WE&H) and Servei d'Ecopatologia de Fauna Salvatge (SEFaS), Dept de Medicina i Cirurgia Animals, Facultat de Veterinària, Univ. Autònoma de Barcelona, Barcelona, Spain. – M. C. Arnal (<https://orcid.org/0000-0002-6770-3400>) and D. Fernández de Luco (<https://orcid.org/0000-0003-3289-4267>), Dept of Animal Pathology, Univ. of Zaragoza, Zaragoza, Spain. – B. Crestanello (<https://orcid.org/0000-0003-1610-8692>), H. C. Hauffe (<https://orcid.org/0000-0003-3098-8964>) and F. Lioce, Conservation Genomics Research Unit, Centre for Research and Innovation, Fondazione E. Mach, S. Michele all'Adige (TN), Italy. – J. Espunyes (<https://orcid.org/0000-0002-8692-1593>), Wildlife Conservation Medicine Research Group (WildCoM), Dept of Animal Medicine and Surgery, Univ. Autònoma de Barcelona, Bellaterra, Spain. – S. Friedrich, Wildlife Research Unit (WFS), Agricultural Center Baden-Württemberg (LAZBW), Aulendorf, Germany and Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology, Univ. of Goettingen, Göttingen, Germany. – D. Gačić (<https://orcid.org/0000-0003-0434-6562>), Dept of Forest Resources Use, Faculty of Forestry, Univ. of Belgrade, Belgrade, Serbia. – L. Grassi, Dept of Animal Medicine, Production and Health (MAPS), Univ. of Padua, Legnaro, Italy. – K. Kavčić (<https://orcid.org/0000-0002-2907-3911>), A. Rezić (<https://orcid.org/0000-0001-6643-7895>), S. Stipoljev (<https://orcid.org/0000-0003-4635-6777>) and N. Šprem (<https://orcid.org/0000-0002-3475-6653>), Faculty of Agriculture, Dept of Fisheries, Apiculture, Wildlife Management and Special Zoology, Univ. of Zagreb, Zagreb, Croatia. – A. Kinser and C. Miller, Deutsche Wildtier Stiftung, Hamburg, Germany. – S. Grignolio (<https://orcid.org/0000-0002-0786-2004>) and FL, Dept of Life Sciences and Biotechnology, Univ. of Ferrara, Ferrara, Italy. – A. Malagnino (<https://orcid.org/0000-0002-6583-700X>), Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LÉCA, Grenoble, France and Dept of Biosciences, College of Science, Swansea Univ., Swansea, UK. – W. Peters (<https://orcid.org/0000-0002-7105-428X>), Dept of Biodiversity, Conservation and Wildlife Management, Bavarian State Inst. of Forestry, Freising, Germany. BP also at: Slovenian Forestry Inst., Ljubljana, Slovenia. – R. Reiner (<https://orcid.org/0000-0003-1016-9347>), Inst. of Wildlife Biology and Game Management, Univ. of Natural Resources and Life Sciences, Vienna, Austria and Berchtesgaden National Park, Berchtesgaden, Germany. – Y. Yankov, Faculty of Agriculture, Dept of Biology and Aquaculture, Trakia Univ., Stara Zagora, Bulgaria. – T. Zwijacz-Kozica (<https://orcid.org/0000-0002-7488-975X>), Tatra National Park, Zakopane, Poland.

Wildlife Biology

2022: e01025

doi: 10.1002/wlb3.01025

Subject Editor: Klemen Jerina

Editor-in-Chief: Ilse Storch

Accepted 24 March 2022



www.wildlifebiology.org

© 2022 The Authors. Wildlife Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

The chamois *Rupicapra* spp. is the most abundant mountain ungulate of Europe and the Near East, where it occurs as two species, the northern chamois *R. rupicapra* and the southern chamois *R. pyrenaica*. Here, we provide a state-of-the-art overview of research trends and the most challenging issues in chamois research and conservation, focusing on taxonomy and systematics, genetics, life history, ecology and behavior, physiology and disease, management and conservation. Research on *Rupicapra* has a longstanding history and has contributed substantially to the biological and ecological knowledge of mountain ungulates. Although the number of publications on this genus has markedly increased over the past two decades, major differences persist with respect to knowledge of species and subspecies, with research mostly focusing on the Alpine chamois *R. r. rupicapra* and, to a lesser extent, the Pyrenean chamois *R. p. pyrenaica*. In addition, a scarcity of replicate studies of populations of different subspecies and/or geographic areas limits the advancement of chamois science. Since environmental heterogeneity impacts behavioral, physiological and life history traits, understanding the underlying processes would be of great value from both an evolutionary and conservation/management standpoint, especially in the light of ongoing climatic change. Substantial contributions to this challenge may derive from a quantitative assessment of reproductive success, investigation of fine-scale foraging patterns, and a mechanistic understanding of disease outbreak and resilience. For improving conservation status, resolving taxonomic disputes, identifying subspecies hybridization, assessing the impact of hunting and establishing reliable methods of abundance estimation are of primary concern. Despite being one of the most well-known mountain ungulates, substantial field efforts to collect paleontological, behavioral, ecological, morphological, physiological and genetic data on different populations and subspecies are still needed to ensure a successful future for chamois research and conservation.

Keywords: behavior, conservation, ecology, genetics, life history, *Rupicapra*, taxonomy, wildlife diseases

Background

The chamois *Rupicapra* spp. is a member of the family Bovidae, subfamily Caprinae, which includes species adapted to mountainous environments. The subfamily may be further divided into different tribes, depending on the classification system (cf. Simpson 1945, Hassanin et al. 2009); however, the taxonomy of mountain ungulates remains largely unsolved. Irrespective of classification subtleties, mountain ungulates inhabit areas that make them particularly susceptible to environmental variations due to, e.g. land use and climate change. Among the Caprinae species, however, the chamois possibly shows the highest behavioral plasticity, which has allowed the genus to occupy a vast area, making it one of the most iconic mammals inhabiting the mountainous regions of Europe and the Near East, as well as an intriguing species for ecological investigations.

Currently, the most accepted classification, based on a combination of morphometric, genetic and behavioral characteristics, considers two species: the northern chamois *R. rupicapra* and the southern chamois *R. pyrenaica* that are further subdivided into seven (*cartusiana*, *rupicapra*, *balcanica*, *tatica*, *carpatica*, *caucasica* and *asiatica*) and three (*ornata*, *parva* and *pyrenaica*) subspecies, respectively (cf. Masini and Lovari 1988, Corlatti et al. 2011). The most abundant subspecies, the Alpine chamois *R. r. rupicapra*, is distributed throughout the Alps and is assessed as least concern by the IUCN. Most other subspecies are only present in limited areas where they face several threats, including poaching, overhunting, human disturbance, competition with livestock, habitat loss and degradation, infectious diseases, hybridization with introduced individuals of other subspecies, and climate change. Addressing these conservation issues relies not only on available knowledge of chamois biology, but also on the identification of future research priorities. A recent review of chamois biology is available in Corlatti et al. (2022a), while

conservation status of both species has been recently assessed by Herrero et al. (2020) and Anderwald et al. (2021); however, to date, the literature lacks compelling insights into future research challenges. In this paper, experts from across Europe outline the state of chamois science, as discussed at the 3rd *Rupicapra* Symposium held online from Makarska (Croatia) in 16–18 June 2021, focusing on research trends and on key aspects of taxonomy and systematics, genetics, life history, ecology and behavior, physiology and disease, management and conservation. The goal of this communication is to provide a state-of-the-art overview of research trends, as well as the most challenging issues in chamois research and conservation.

Research trends

The study of chamois has a longstanding history. Much of our current knowledge is owed to the pioneering work of Camerano (1914), Couturier (1938), Krämer (1969) and Schröder (1971), among others. Since then, research activity has flourished, greatly increasing our understanding of the biology of chamois species and subspecies. Research contributions, however, are not evenly distributed over time and across taxa. As Fig. 1 shows, the number of peer-reviewed scientific articles focusing on chamois has increased markedly over the past 40 years, with a 273% increase after the year 2000 and has stabilized since 2010, for a total of 756 publications (see Supporting information for the list of publications, and for a description of the methodological approach to data collection and analysis).

With respect to the trend in the number of chamois publications in proportion to those on Caprinae, publications increased more rapidly for chamois than for mountain ungulates as a whole, and chamois publications accounted for 16% of all Caprinae publications in the study period (Fig. 2).

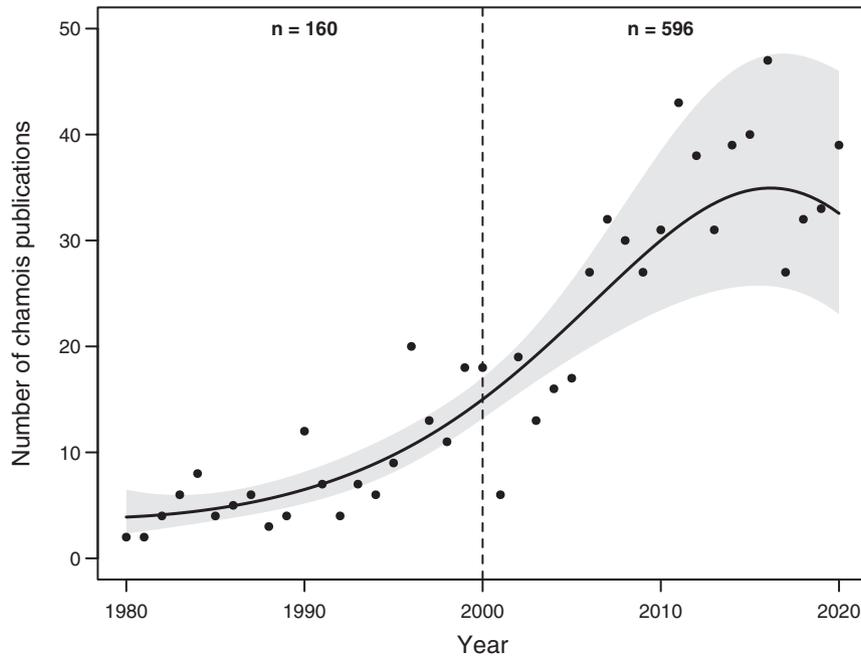


Figure 1. Number of peer-reviewed publications on chamois *Rupicapra* spp., between 1980 and 2020. The fitted line shows the expected response of a 3rd level polynomial autoregressive Poisson model; the shaded area indicates the 95% confidence level. The dashed line separates the first from the last two decades (midyear 2000 used as midpoint).

Major biases emerged in the number of publications when species and subspecies were taken into account, although these broadly reflect the relative abundance of each species/subspecies (cf. abundance data in Corlatti et al. 2022a). About 80% of all chamois publications between 1980 and 2020

mentioned the northern chamois *R. rupicapra* (n=608), while the southern chamois *R. pyrenaica* was mentioned in only 28% (n=208). Differences were even more evident when considering subspecies. For the same time frame, only 8.2% (n=50) of the publications on the northern

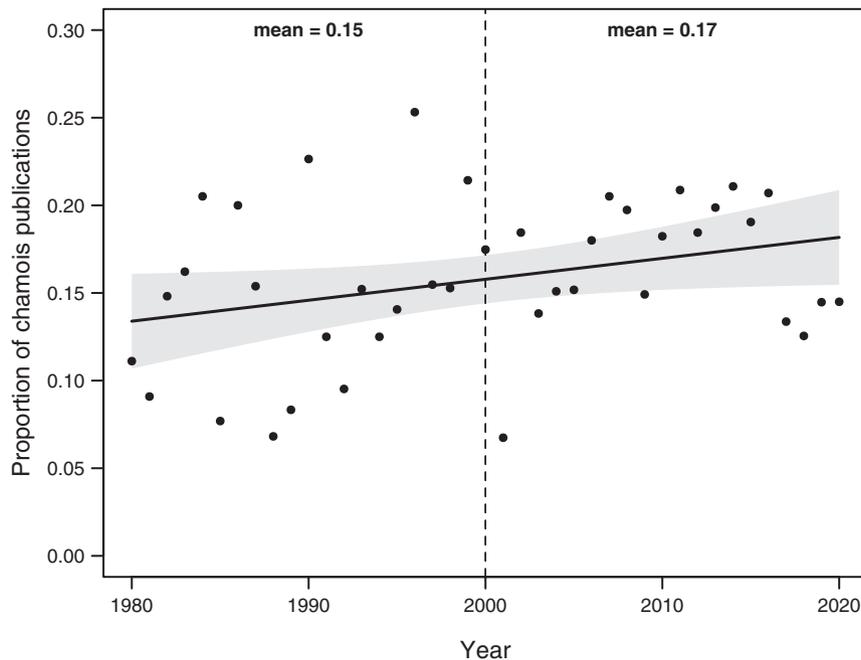


Figure 2. Proportion of publications on chamois with respect to publications on all Caprinae species, between 1980 and 2020. The fitted line shows the expected response of a Gaussian linear model; the shaded area shows the 95% confidence level. The dashed line separates the first from the last two decades.

chamois considered subspecies other than the Alpine one, i.e. *R. r. cartusiana* = 0.5% (n=3), *R. r. tatrica* = 3.6% (n=22), *R. r. carpatica* = 0.2% (n=1), *R. r. balcanica* = 2.3% (n=14), *R. r. asiatica* = 0.3% (n=2), *R. r. caucasica* = 1.3% (n=8). The situation appears more balanced for the southern chamois subspecies, with *R. p. parva* and *R. p. ornata* accounting for 27.9% (n=58) of all *pyrenaica* publications, or 12.0% (n=25) and 15.9% (n=33), respectively).

When analyzed by topic, we found that veterinary sciences have clearly dominated chamois research in the last four decades, involving about one third of all publications (Table 1). Genetics, behavior and life history also accounted for a large proportion (in total, over 50%) of the *Rupicapra* literature. Taxonomy and systematics were the least studied (ca 4%), although the low percentages for movement ecology and population dynamics (ca 9 and 6%, respectively) were perhaps even more surprising, given the importance of these disciplines for management and conservation (a topic mentioned explicitly in 17% of publications). However, in the recent *Rupicapra* symposium, these values were much different: of the 49 contributions, only about 10% concerned genetics, taxonomy and systematics (n=5), while life history, ecology and behavior had the highest number of contributions (39% (n=19)); physiology and disease covered 24% (n=12), and management and conservation, 27% (n=13).

The state-of-the-art knowledge and knowledge gaps for each topic illustrated in Table 1 are described in greater detail in the following sections. Emphasis is on the main challenges for the future of chamois research and conservation, and only the most recent and/or relevant articles are cited.

Taxonomy and systematics

Chamois taxonomy and systematics have been continuously revised since the beginning of the 20th century. Over the years, authorities such as Neumann, Lydekker, Camerano and Couturier expressed different views about the taxonomic status of *Rupicapra*, supporting classifications based on morphology for one, two or even three distinct species (cf.

Corlati et al. 2022a). Much of the current taxonomy is owed to the works of Lovari and Scala (1980) and Nascetti et al. (1985), that, based on morphometric and electrophoretic data, support a subdivision into two species: the southern chamois *R. pyrenaica*, and the more recent northern chamois *R. rupicapra*. These species colonized Europe in successive waves, possibly from eastern Europe (Masini and Lovari 1988). The debate was reignited with the advent of molecular methods: initial phylogenies based on mitochondrial DNA revealed not two, but three very old clades (from the early Pleistocene, 1.9 Mya) with a clear geographic signal (Crestanello et al. 2009, Rodríguez et al. 2009), one for each of the morphological species. Nuclear markers (e.g. microsatellites, melanocortin-1 receptor gene, introns) also clustered populations into three groups, but these groups did not align in a simple way with mitochondrial lineages. Pérez et al. (2017) suggested that the patterns of differentiation for various molecular markers in chamois are best explained as reticulate evolution. Recent analyses of complete mitochondrial genomes (Iacolina et al. 2021) supported the subdivision into three clades: two corresponding to the classical species *R. pyrenaica* and *R. rupicapra*, and a third including the subspecies *R. p. ornata* and *R. r. cartusiana*.

This long-lasting controversy raises the question of whether chamois taxonomy will ever be resolved. Although most of the recent literature relies on the use of molecular tools, the inconsistencies in the molecular systematics outlined above suggest that analysis of a limited number of markers will not suffice to solve this issue in chamois. Phylogeny and phylogeography derived from a single marker gene, protein sequence and non-coding regions reflect only the evolution of that particular DNA segment. Consequently, the use of a single or several markers has led to problems of interpretation, since other chamois genes may have different rates of evolution, and different genes accumulate mutations at different rates. Phylogenetic analysis comparing results from modern and ancient specimens could help to map the complex evolutionary history of chamois by better estimating mutation rates for different markers; in addition, genomic analyses of a representative number of individuals from each subspecies will likely improve our understanding (see next

Table 1. Chamois publications by topic from 1980 to 2020. The search statement used for each topic and the percentage (with absolute number in parentheses) of publications by topic with respect to the total number of *Rupicapra* publications (n=756) are indicated. Percentages sum to > 100% and numbers to > 756 because the same publications may be tagged under multiple topics.

Topic	Search statement	% of all chamois publications
Taxonomy and systematics	'rupicapra' AND 'taxonomy' OR 'systematics'	4.1 (n=31)
Genetics	'rupicapra' AND 'genetic' OR 'DNA'	20.5 (n=155)
Life history	'rupicapra' AND 'growth' OR 'reproduction' OR 'survival'	13.4 (n=101)
Ecology and behavior	'rupicapra' AND 'population dynamics'	6.0 (n=45)
	'rupicapra' AND 'predation' OR 'competition'	10.1 (n=76)
	'rupicapra' AND 'behavior' OR 'mating' OR 'social'	18.0 (n=136)
	'rupicapra' AND 'diet' OR 'foraging'	9.9 (n=75)
	'rupicapra' AND 'home range' OR 'movement' OR 'dispersal' OR 'habitat selection'	9.4 (n=71)
Physiology and disease	'rupicapra' AND 'physiology' OR 'disease' OR 'parasites'	36.5 (n=276)
Conservation and management	'rupicapra' AND 'conservation' OR 'protection' OR 'management'	16.8 (n=127)

section). To support taxonomics below the species level, however, a clearer understanding of chamois evolutionary history is needed, but this will require contributions from other fields of research such as paleontology, morphology and behavior.

Notably, despite its importance for elucidating the evolutionary history of chamois, no paleontological research was presented or discussed during the third chamois meeting, although ancient DNA studies are ongoing. The earliest fossil of chamois dates back to some 800 000 years ago, in eastern Europe, but the species remains unidentified (Fernandez and Crégut 2007); therefore, it is likely that the chamois has been present in eastern Europe from the end of the Early Pleistocene. Instead, the oldest fossil associated with *R. pyrenaica*, from the southern French Pyrenees, is 440 000 years old (Rivals 2004). Therefore, although the two extant species were both in Europe at the beginning of the Würm glaciations, the northern chamois failed to colonize the southernmost areas, making them a refuge for the southern species (Masini and Lovari 1988). More paleontological material is needed to clarify the evolutionary history of the chamois, and of mountain ungulates in general, a challenging task limited by the scarcity of fossil records in mountains (Schaller 1977).

In conclusion, although taxonomy is often considered particularly relevant to chamois population management, and large-scale decision making would undoubtedly benefit from a well-defined taxonomic classification, we caution against relying on interpretations drawn from individual tools, either behavioral, morphological, paleontological or genetic/genomic, as results are intrinsically probabilistic, and partial at best. Furthermore, regardless of the taxonomic status assigned, we suggest the value of single chamois populations should be also assessed at the historical and conservation levels (Corlatti et al. 2011).

Genetics

Various neutral molecular markers (mitochondrial genes, microsatellite markers, sex-determining Y genes) have been

used to study phylogeny, population genetic structure, hybridization, demographic history and local adaptation in chamois. Traditional neutral markers (such as microsatellites) indicate that the Alpine chamois *R. r. rupicapra* has high values of genetic diversity for almost all markers analyzed, while the Apennine chamois *R. p. ornata* shows an extremely low level of genetic diversity; most other chamois subspecies show intermediate values. More recently, coding regions (e.g. major histocompatibility complex, MHC) and the simultaneous analysis of a large number of genomic markers (single nucleotide polymorphisms, SNPs) have been used to gain more detailed insight into the adaptive genetic diversity and evolutionary potential of the species (Pérez et al. 2014).

Application of recent advances in genomic technologies could provide even more valuable information. For example, given the ongoing taxonomic controversies mentioned in the previous section, combining available data with the analysis of whole genomes could give us a better understanding of the evolutionary relationships within the genus *Rupicapra* (Fig. 3). In addition, non-invasive genetic monitoring of chamois using environmental DNA (eDNA, e.g. feces, urine, hair, etc.) could be used to establish and monitor management and conservation units and to provide the basis for decisions concerning the maintenance of chamois evolutionary potential. Finally, the genetic analysis of ancient samples (e.g. whole mtDNA sequencing) would enable the evaluation of genetic loss and changes over time associated with population dynamics and evolutionary processes.

Genetic and genomic methods should also be applied to determine the impact of human-induced changes in climate and land use on chamois populations, as these are likely to be complex and involve multiple biotic and abiotic factors (Vitasse et al. 2021). For example, adaptation to shifts in vegetation and changing interspecific interactions can be studied through diet, traditionally analyzed from field observation or through microscopical analysis of fecal pellets or stomach contents. However, the simultaneous taxonomic identification of all dietary items can now be performed using DNA extracted from fresh fecal pellets (through ‘metabarcoding’ or ‘metataxonomics’). Similarly, the effect of dietary, behavioral or environmental changes on health can be implied through

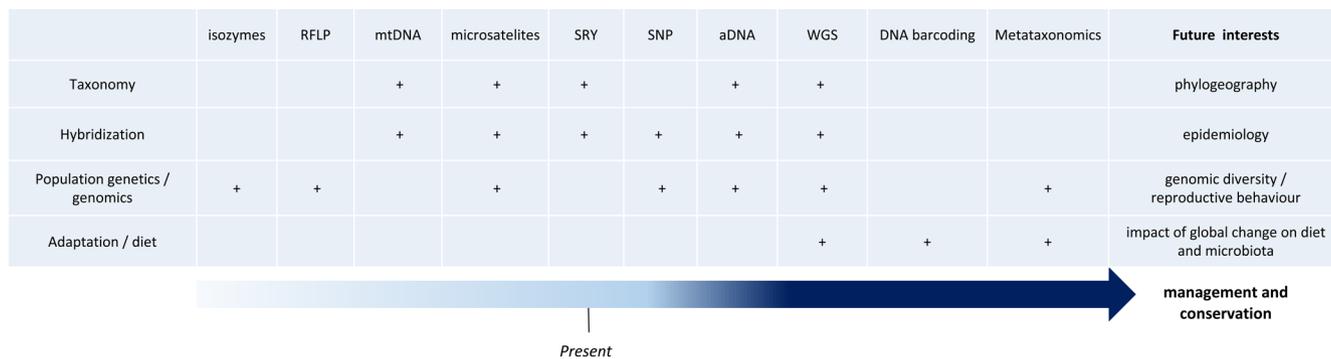


Figure 3. Flowchart linking management and conservation issues relevant to chamois that can be addressed using molecular markers and approaches (currently available or under development) and their potential future applications.

the study of the gut microbiota (e.g. helminths) and microbiota composition (bacteria, fungi and viruses). Changes in the microbiota are known to influence an individual's ability to adapt to alterations in the environment with consequent implications on health, survival and possibly fitness (Hauffe and Barelli 2019).

Technological advances in conservation genomics now make it possible to answer new and relevant questions, such as 'Which genes are under selection?', 'What are the genes associated with specific traits?', 'Are these changes associated with adaptation or other natural processes?'. In fact, high quality genome-scale data could increase the precision of traditional parameters such as genetic diversity, mutation rate and effective population size, provide better understanding of the mechanisms that allow chamois to adapt to a changing environment, as well as improve species conservation efforts.

In addition, whole genome technologies could clarify the impact of hybridization on conservation status, since hybridization between species or subspecies, resulting from legal and illegal translocations of chamois, could lead to the loss of local adaptation to particular niches. Despite awareness of this risk for over a decade (Crestanello et al. 2009), evidence of recent hybridization has only been reported between different subspecies of *R. rupicapra* in regions where chamois have been introduced for hunting purposes (reviewed by Iacolina et al. 2019), even though hybridization between other chamois taxa is suspected. Therefore, cases of hybridization in chamois should be identified and their consequences monitored, possibly using whole genome studies to distinguish gene introgression from hybridization.

Genetic and genomic markers are powerful tools for answering many management questions, and may be more cost effective and rapid than intensive field work. Wildlife practitioners should be made aware of the availability of different markers and approaches, the questions that can be answered, and the type and number of samples required for their application, as well as costs, so that these tools can be applied effectively, keeping in mind that for some management questions traditional markers/approaches will still be more efficient.

Life history

Research on chamois life history traits is mainly limited to the Alpine subspecies *R. r. rupicapra* and, to a lesser extent, the Pyrenean chamois *R. p. pyrenaica*. Further efforts are needed to answer several open questions on growth, reproduction and survival. Chamois of all subspecies are nearly monomorphic, with the notable exception of a seasonal sexual dimorphism in body mass just before the rut in late autumn, when males are notably heavier than females (Rughetti and Festa-Bianchet 2011). The evolutionary meaning of this dimorphism is unclear, but it may indicate a high investment in male-male mating competition, allowing adult males to lose more than 15% of their body mass during the rut, while maximizing their probability of overwinter survival

(cf. Ferretti et al. 2014, Apollonio et al. 2020). Interestingly, the extent of mass loss during the rut is age- and site-specific (Mason et al. 2011); therefore, it would be worth investigating how environmental heterogeneity influences sex- and age-specific patterns of body mass, and how mass is associated with the opportunity for sexual selection (below) and the probability of survival. Increasing evidence for ecological plasticity in chamois (Reiner et al. 2021) also raises the question of species-specific resilience towards climate and other environmental changes. While a decline in body mass with increasing summer temperature has been reported, the response may be conditional on the possibility of choosing habitats where it may be possible to overcome the negative effects of increasing temperatures, as in the case of open alpine areas versus forests (Reiner et al. 2021). Alongside the opportunity to investigate site-specific variations in compensatory growth (Rughetti and Festa-Bianchet 2010) and its possible trade-off with reproductive success and survival, the effects of body mass variations is one of the most promising research areas, as it has obvious evolutionary relevance, and should be analyzed from morphological, behavioral and physiological perspectives.

The intense competition among males during the rut, and their significant loss in body mass, would suggest a high level of polygyny, yet there appears to be a low level of this reproductive strategy (Corlatti et al. 2015a). Thus far, however, no conclusive data have been collected; as for most other Caprinae, variance in male reproductive success is unknown and consequently, the level of polygyny of chamois is still debated. The degree of polygyny can be quantified through the intensity of sexual selection on males, I_m , the variance in male reproductive success divided by the square of the mean reproductive success (Arnold and Wade 1984). As shown in other ungulate species, behavioral and genetic I_m often differ from each other, and this may be particularly true for bovids, where copulations can be repeated, and ejaculations are not obvious. Consequently, future studies should combine the collection of observational data from marked populations with genetically determined paternity data (even though sampling most kid-mother dyads and all potential fathers may be difficult) since the usefulness of I_m is critical both from an evolutionary and applied perspective, as knowledge of this parameter could improve management of hunted populations, where the age-sex structure is often skewed towards younger individuals and females. Variation occurs not only between, but also within mating systems: alternative male mating tactics in chamois – territorial and non-territorial – have been widely studied (von Hardenberg et al. 2000, Corlatti et al. 2012a), but some fundamental questions remain. For example, while other mountain ungulates may switch tactics in adverse environmental and climatic conditions, e.g. with deep snow cover (Alpine ibex *Capra ibex*: Apollonio et al. 2013), in chamois the adoption of a given tactic appears less flexible, though its benefits and costs can change with weather stochasticity (Corlatti et al. 2020). The mechanisms allowing the coexistence of alternative tactics, however, are still largely unknown. For example, it is unclear

whether such tactics are frequency-dependent or, as shown in other mountain ungulates, condition-dependent and if so, whether they reflect individual characteristics, or specific exogenous conditions. More generally, a more comprehensive evaluation of the role of environmental factors on the chamois mating system is needed, including the influence of the environment (e.g. open alpine areas versus forests), as observed in other ungulate species with mating system polymorphism, such as fallow deer *Dama dama* (Thirgood 1991).

Although there is increasing evidence of unbiased sex-specific survival (Gonzalez and Crampe 2001, Bocci et al. 2010, Corlatti et al. 2012b), for many subspecies this information is completely unknown. Furthermore, the pattern of age-specific survival in both sexes (Loison et al. 1999), how this changes with environmental heterogeneity, and the trade-off between survival and other traits such as body mass, horn size or reproductive success are not fully understood (Tettamanti et al. 2015, Corlatti et al. 2017). The determinants of the survival of specific sex- and age classes and how their impact may change with different environments and demographic conditions also require investigation, yet are key to chamois management. For example, high survival of kids is crucial in driving the demographic trend of chamois populations in face of climatic changes (Lovari et al. 2020, Chirichella et al. 2021). Given the scarcity of data on this topic, and on the survival of all demographic classes in general, a comparative analysis of data from different populations and possibly different Caprinae species, is urgently needed to enable proactive and sustainable population management, as well as to interpret data linked to the benefits and costs of different reproductive tactics.

Ecology and behavior

Published accounts of some aspects of chamois ecology and behavior are surprisingly scarce, yet are key to chamois conservation. For example, environmental change, interspecific competition, the return of predators and increased human disturbance may interact to create a dynamic scenario affecting the behavior and ecology of chamois, and still need to be fully elucidated.

Chamois feeding ecology is well known, at least at the local scale. Chamois have been previously classified as intermediate feeders (Hofmann 1989), and more recently as cattle-type feeders on the basis of their intraruminal papillation (Clauss et al. 2009). Grasses are key dietary components, especially in summer (Espunyes et al. 2019a), but woody species could also be important. Their importance for chamois survival is expected to be spatially heterogeneous: woody plants are only consumed during periods of fasting (e.g. winter) in some areas, but are core components of chamois diet in others (e.g. common heather *Calluna vulgaris* in eastern Pyrenees: Espunyes et al. 2019a). Consequently, as the ongoing shrubification of secondary grasslands is expected to reduce grass availability in open mountainous landscapes (Espunyes et al. 2019b), the potential for colonizing

woody plants to compensate for reduced nutritional intake requires investigation. Habitat modifications such as wood encroachment and successional changes in secondary meadows may also interact with climatic changes and impact chamois life history traits by, e.g. improving feeding conditions in spring (Espunyes et al. 2021). However, the effects of such changes on chamois feeding ecology are complex, and may be critical to recruitment. For example, early onset of vegetation green-up may mismatch with weaning, which is when juveniles depend on fresh nutritious vegetation, impacting their survival (Lovari et al. 2020). At the same time, climate change may significantly alter forest dynamics, by increasing the frequency and magnitude of natural disturbances (Senf and Seidl 2021), possibly leading to improved foraging opportunities in forested areas due to reduced tree cover (Vavra and Riggs 2010).

Feeding ecology is tightly related to spatial ecology; therefore, collecting high-quality environmental and vegetational data using satellite telemetry will help to disclose fine-scale patterns of forage selection (cf. Duparc et al. 2020). More generally, the chamois is a potential candidate for mapping environmental changes, since in this species, altitudinal shifts, changes in habitat use or behavior (e.g. in circadian and circannual activity rhythms: Brivio et al. 2016), are expected in response to climate and land use changes. Recent studies suggest site-specific responses to environmental changes, likely mediated by local conditions (cf. Ciach and Pęksa 2019). Unfortunately, however, information on chamois spatio-temporal behavior is limited and the scarcity of replicates often makes it difficult to extrapolate the results of local studies to other populations. Chamois social behavior, including grouping patterns, intra-sexual aggression or mother-offspring relationships, has been quite extensively investigated but mostly in the Alpine, Pyrenean and Apennine subspecies (Corlatti et al. 2022a). One of the best-known aspects of chamois behavior is male mating behavior, where alternative reproductive tactics have been locally reported, although the suggested ecological mechanisms of their long-term co-occurrence (Lovari et al. 2006, Corlatti et al. 2015a, 2020, cf. 'Life History') require support from studies conducted in different areas. On the other hand, there is an urgent need for information on key aspects of female behavior, including habitat selection, ranging movements, dispersal and reproductive behavior. More generally, investigating differences in behavioral patterns at specific and subspecific levels may improve understanding of the impact of local environmental conditions on chamois social behavior (cf. Kavčič et al. 2021a) and, more broadly, the eco-evolutionary patterns leading to the morphological and behavioral variation typical of the Caprinae subfamily (cf. Schaller 1977).

Future management decisions will also depend on a better understanding of the relationships between chamois and other species. For example, while the potential effects of interspecific competition between chamois and red deer *Cervus elaphus* (Ferretti et al. 2015) or European mouflon *Ovis aries musimon* (Chirichella et al. 2013), as well as interactions

with livestock (Mason et al. 2014) have been assessed for some populations, they may vary substantially among sites (Corlatti et al. 2022a). As prey species, the contribution of chamois to the diet of gray wolf *Canis lupus* (Mori et al. 2017) or Eurasian lynx *Lynx lynx* (Molinari-Jobin et al. 2007) has been evaluated locally, but the demographic impact of predators on chamois populations at large remains unknown.

Finally, given the impact of global change on mountain ecosystems, future chamois research should focus on the effects of environmental changes on a number of ecological and behavioral aspects. Information gaps on chamois ecology and behavior especially concern taxa other than *R. r. rupicapra*, *R. p. pyrenaica* and *R. p. ornata*. For example, most information on life history consequences of climate change derives from Alpine or Apennine studies (cf. Lovari et al. 2020, Corlatti et al. 2022a). Furthermore, the mechanistic link between increasing temperature and chamois responses is unclear, and chamois may be influenced directly (i.e. through effects on behavior) or indirectly (i.e. through effects on resources) (Lovari et al. 2020, Reiner et al. 2021).

Physiology and diseases

The interest in chamois health and parasitology is longstanding, with contributions dating to the 19th century. However, it was only in the 1960s and 1970s that academic groups (namely in Bern, Vienna, Ljubljana, Turin and Lyon) focused with greater continuity on the diversity and quantitative characterization of the helminth communities of *R. rupicapra*. Several decades later, the etiological, physio-pathological and epidemiological investigation of keratoconjunctivitis (IKC) (Grattarola et al. 1999, Degiorgis et al. 2000, Arnal et al. 2013) and sarcoptic mange outbreaks in chamois (Rossi et al. 1995, Fernández-Morán et al. 1997) were investigated. In the early 1990s, the onset of pestivirus by genotype 4 of the border disease virus (BDV-4) (Alzieu et al. 2004, Arnal et al. 2004, Hurtado et al. 2004), a novel outbreak disease in *R. p. pyrenaica*, promoted a more integrative approach for health assessments of chamois populations.

In the 2000s, research on chamois disease benefitted from the increasing availability of advanced fit-to-purpose diagnostic and analytical tools, to explore the intraspecific variability of major chamois pathogens and their molecular-based epidemiology, including cross-transmission opportunities at the interface with livestock or sympatric wildlife (Luzzago et al. 2016, Fernández-Aguilar et al. 2017). In parallel, passive and active disease surveillance was fruitfully integrated into long-term studies of chamois ecology using marked populations, which allowed the development of population models to address conservation-oriented debates and disease mitigation measures (Serrano et al. 2015). An example of this integrative approach was the demonstration of the spontaneous extinction, approximately two decades from onset, of the much-feared BDV-4 pestivirus in the intensively monitored chamois population of Orlu, in the French Pyrenees (Gilot-Fromont et al. 2018). Equally

interesting was the description of the link between IKC spread and the herd-specific social behavior of females (Gelormini et al. 2017). These results suggested the need for multidisciplinary research to understand outbreak dynamics in the notoriously susceptible wild *Rupicapra* populations.

Despite these remarkable advances in chamois health research, many other questions are waiting to be explored. With few exceptions, there is a lack of descriptive and experimental trials to explore the underlying mechanisms responsible for differences in immune responses (e.g. genetic background, coinfections, resource availability and quality, geology, population density or social stress among others), which could explain why some social units or populations are more resilient to the effects of outbreak diseases than others, despite sharing the same or neighboring mountain ranges. In addition, factors explaining the shift from the epidemic to the endemic status of persisting pathogens (e.g. sarcoptic mange) are unknown for chamois. Both knowledge gaps negatively impact the adoption of research-based chamois-pathogen(s) coexistence strategies by wildlife managers. The bias towards a limited number of *Rupicapra* subspecies (namely *R. r. rupicapra*, *R. p. pyrenaica* and, to a lesser extent, *R. r. tatraca*, *R. p. ornata* and *R. p. parva*) is also notable and should be addressed. In fact, very recently, tick vectors, tick-borne diseases and endoparasites have been studied in *R. r. rupicapra* but also the poorly investigated *R. r. balcanica*; this research provided new insights into chamois parasitological status and tick infestation of the Balkan chamois (Yankov et al. 2021). By combining parasitological and infectious disease studies, other authors also reported an unexpectedly high prevalence of tick-borne *A. phagocytophilum*, including zoonotic strains, in Alpine chamois of the eastern Italian Alps (Grassi et al. 2021). These two examples illustrate that chamois throughout Europe may harbor and suffer from known parasitological and viral diseases as well as those caused by emerging pathogens, such as tick-borne pathogens; thus, increased and standardized screening is recommended wherever possible.

Finally, more effort should be devoted to exploring the relationships between climate/environmental changes and the dynamics of chamois pathogens, with respect to current/expected hosts, pathogen and vector shifts and related conservation threats.

Conservation and management

The conservation status of the genus *Rupicapra* is favorable: both the northern and the southern species are abundant and have been increasing in number and range (particularly towards low altitudes) from the second half of the 20th century. However, five of the 10 subspecies are threatened, three are decreasing in population size or range, and even some populations of the most abundant subspecies (e.g. *R. r. rupicapra*, *R. p. parva* and *R. p. pyrenaica*) have started to decline (Herrero et al. 2020, Anderwald et al. 2021). Overall, more detailed and up-to-date information on abundance and

Table 2. Status of chamois throughout its distribution range. Conservation threats are scale- and context-dependent – CB: lack of cross border coordinated management; CC: climate change; CL: competition with livestock; CW: competition with wild ungulates; D: diseases; G: interbreeding with Alpine chamois *R. r. rupicapra*; HL: habitat loss; OH: over harvesting; P: poaching; PS: small population size (Shackleton et al. 1997, Herrero et al. 2020, Anderwald et al. 2021). ¹ This includes ~100 chamois hybridized with Alpine chamois living in the Low Tatras. ² Proposal by Anderwald et al. (2021). ³ Indicates that translocations have occurred for the relevant species and subspecies.

	Number	Trend	Threats	CITES appendix	Habitat directive annexes	Bern convention appendix	IUCN 2020–2021	Translocations
Northern chamois <i>R. rupicapra</i>	~550 000	Stable (?)	CL, CW, D, G, HL, OH, P, PS		V	III		+ ³
Chartreuse chamois <i>R. r. cartusiana</i>	1500	?	CL, G, HL, OH, P				VU, D1+2	
Alpine chamois (Alps) <i>R. r. rupicapra</i>	~ 500 000	Stable (?)	CC, CW, D, HL, OH					+
Balkan chamois <i>R. r. balcanica</i>	< 10 000	?	CB, CL, G, HL, P		II, IV			+
Tatra chamois <i>R. r. tatrica</i>	1100 ¹	↑	D, P, PS		II, IV		EN, B1+2ab	+
Carpathian chamois <i>R. r. carpatica</i>	8000	?	CL, P					
Caucasian chamois <i>R. r. caucasica</i>	> 9000	?	CL, CW, P				VU, C1	
Anatolian chamois <i>R. r. asiatica</i>	800	?	CL, CW, HL, P				EN, C1+2a(i) ²	
Alpine chamois (New Zealand) <i>R. r. rupicapra</i>	> 18 500	↑						
Southern chamois <i>R. pyrenaica</i>	71 500	?	CC, CL, CW, D, HL		V	III	LC	+
Apennine chamois <i>R. p. ornata</i>	2500	↑	CC, CL, CW, HL	II	II, IV	II	VU	+
Cantabrian chamois <i>R. p. parva</i>	16 000	?	CC, D, HL					+
Pyrenean chamois <i>R. p. pyrenaica</i>	53 000	?	CC, D, HL					+
Total	~ 620 000	?	CC, CL, CW, D, G, HL, OH, P, PS					+

distribution is required, especially for the least-known subspecies (cf. ‘Research trends’).

The main conservation challenges are summarized in Table 2. To address these, action plans with concrete conservation measures, mainly involving the implementation of hunting regimes with respect to age- and social structure, establishment of protected areas and game reserves, and regular population monitoring (e.g. using traditional count or molecular methods) have been partially implemented, but are still lacking for several subspecies and regions. Regardless of geographical scale and taxonomic status, effective conservation and management of chamois principally benefits from the collection of rigorous periodic data on population size, age-sex structure and distribution. Currently, this information is mainly obtained using block counts which, despite underestimating true size and presence, particularly in forested habitats (Corlatti et al. 2015b), may provide useful trend data if conducted over several years in a standardized manner and environmental conditions affecting detection remain stable (cf. Reiner et al. 2020). However, other monitoring methods could be used to provide estimates of population size and/or distribution, including, e.g. distance sampling, density-dependent biometric indices, population reconstruction,

camera traps and GPS-tracking (Kavčić et al. 2021b). The use of non-invasive molecular approaches using eDNA from fecal samples combined with classical or spatially-explicit capture–mark–recapture methods are particularly promising, especially in areas where direct observations of chamois are difficult, such as forests. However, the reliability of a given method (that is, the ability to meet the underlying assumptions) may vary depending on local conditions; therefore, future studies should seek to investigate the robustness of different estimators of absolute population size and distribution under different environmental conditions. Furthermore, studies are urgently needed to assess the reliability of relative abundance indices (e.g. block counts, camera trapping rate) to track spatio-temporal variations in population size and allow for the adoption of sustainable field work effort in the long term.

Information on population size and distribution is particularly relevant to active management, as the chamois is hunted throughout most of its distribution range with a variety of hunting regimes that should be based on reliable knowledge of these two parameters. Harvesting plans generally adopt simplified age classes or more sophisticated grouping systems; however, for any given population, conservative harvest

quotas should be decided according to current demographic structure, with the aim of avoiding strong skews in sex- and age-ratios to ensure long-term viability and persistence (cf. Skonhofs et al. 2002), but also to avoid a biased selection of different behavioral traits. Although information on harvest rate is still fragmentary for many subspecies (Damm and Franco 2014), in some populations overharvesting of certain sex- and age-classes, especially adult males, still persists, possibly due to trophy hunting. We caution against these practices which, besides representing a conservation threat, might lead to unintentional artificial selection and disruption of natural evolutionary trajectories. More generally, information on the effects of hunting on chamois is lacking, including the short- and long-term consequences of different hunting regimes on space use, mating behavior, physiology, population structure and demography.

The future of chamois conservation and management will further depend on a number of different factors, with impacts on demography and life history traits that still need to be fully clarified. These include, for example, hybridization among species and subspecies (cf. ‘Genetics’), climate change (cf. ‘Life history’), land use changes and recent ecological changes, mainly with respect to competition with other wild ungulates, predation by carnivores (cf. ‘Ecology and behavior’), and impact of parasites and pathogens (cf. ‘Physiology and disease’). With carefully collected life history data, predictions of future distributions and the sustainability of management interventions could be modeled. It is worth mentioning the importance of translocations, including introductions and reintroductions, which, irrespective of their purpose (including hunting – e.g. New Zealand, Slovakia, Czech Republic or conservation – e.g. Apennines), have played a key role in the recovery of chamois. Translocations are still used to restock and rewild, but should carefully consider the genetic origin of source and host populations, while taking into account the challenges of taxonomic classification (cf. ‘Taxonomy and systematics’). Finally, conflicts between chamois and human-related activities such as forestry should also be addressed. Overall, the browsing impact of the species appears limited, but local and species-specific negative effects have been reported (Kupferschmid et al. 2014). It seems likely that the impact of chamois on forest ecosystems will vary depending on site conditions, population density and hunting regimes, suggesting that a more extensive assessment over multiple populations of subspecies living in different ecological conditions is needed. More generally, a deeper understanding of the impact of chamois and other wild Caprinae species on vegetation, i.e. on forest/grassland ecosystems, will require long-term assessment using appropriate community-based metrics (cf. Nopp-Mayr et al. 2020).

Conclusions

The Caprinae subfamily consists of species with a great diversity of forms and behaviors, the result of complex

eco-evolutionary scenarios favored by radiation towards very different ecological conditions (cf. Schaller 1977). In many respects, the chamois occupies an intermediate position in the evolutionary pathways between forest-dweller, monogamous and monomorphic goat antelopes such as the serow *Capricornis* spp. and highly dimorphic, highly polygynous wild sheep *Ovis* spp. inhabiting open habitats (Geist 1987). Accordingly, the chamois is a very interesting target for ecological investigations, but at the same time a great effort is needed to collect data over large geographical areas to enable the extrapolation of results to other populations.

Research on the genus *Rupicapra* has markedly increased over the last decades, contributing substantially to our knowledge of the biology and ecology of mountain ungulates. However, the majority of chamois publications are focused on populations inhabiting the Alps and, to a lesser extent, the Pyrenees and Apennines. While this bias may be partly explained by the greater abundance of the Alpine and Pyrenean subspecies compared to the others (cf. Herrero et al. 2020, Anderwald et al. 2021), we suggest that the scarcity of replicates from other subspecies and/or geographic areas is limiting the advancement of chamois science and its application to conservation. The importance of environmental heterogeneity in shaping behavioral and life history traits, especially in response to ongoing climatic change, is increasingly evident, and will be one of the biggest challenges for the future of chamois research and conservation. Substantial contributions to this challenge may derive from site-specific quantitative assessment of reproductive success, investigation of fine-scale foraging patterns and dietary variations, and a mechanistic understanding of disease outbreaks and site-specific resilience, which may help clarify the mechanisms of life history trade-offs. From a conservation perspective, the resolution of taxonomic disputes, the estimation of the degree and importance of subspecies hybridization, the assessment of the impact of different hunting regimes, and the adoption of reliable methods for estimating population abundance are issues of primary concern. Overall, substantial field efforts to collect paleontological, behavioral, ecological, morphological, genetic and physiological data on populations from different subspecies and geographic areas are needed to clarify several aspects of the evolutionary biology and ecology of chamois. Mobilization of research groups to expand their work on less-known subspecies, and broader collaboration among experts would greatly contribute to a better understanding of subspecies-specific biology and management, thereby ensuring a successful future for chamois conservation and research.

Author contributions

Luca Corlatti: Conceptualization (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Laura Iacolina:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Toni Safner:** Conceptualization

(equal); Writing – original draft (equal); Writing – review and editing (equal). **Marco Apollonio**: Writing – original draft (equal); Writing – review and editing (equal). **Elena Buzan**: Writing – original draft (equal); Writing – review and editing (equal). **Francesco Ferretti**: Writing – original draft (equal); Writing – review and editing (equal). **Sabine Hammer**: Writing – original draft (equal); Writing – review and editing (equal). **Juan Herrero**: Writing – original draft (equal); Writing – review and editing (equal). **Luca Rossi**: Writing – original draft (equal); Writing – review and editing (equal). **Emmanuel Serrano**: Writing – original draft (equal); Writing – review and editing (equal). **María Cruz Arnal**: Writing – original draft (supporting); Writing – review and editing (supporting). **Francesca Brivio**: Writing – original draft (supporting); Writing – review and editing (supporting). **Roberta Chirichella**: Writing – original draft (supporting); Writing – review and editing (supporting). **Antonella Cotza**: Writing – original draft (supporting); Writing – review and editing (supporting). **Barbara Crestanello**: Writing – original draft (supporting); Writing – review and editing (supporting). **Johan Espunyes**: Writing – original draft (supporting); Writing – review and editing (supporting). **Daniel Fernández de Luco**: Writing – original draft (supporting); Writing – review and editing (supporting). **Saskia Friedrich**: Writing – original draft (supporting); Writing – review and editing (supporting). **Dragan Gacic**: Writing – original draft (supporting); Writing – review and editing (supporting). **Laura Grassi**: Writing – original draft (supporting); Writing – review and editing (supporting). **Stefano Grignolio**: Writing – original draft (supporting); Writing – review and editing (supporting). **Heidi Hauffe**: Writing – original draft (supporting); Writing – review and editing (supporting). **Krešimir Kavčić**: Writing – original draft (supporting); Writing – review and editing (supporting). **Andreas Kinser**: Writing – original draft (supporting); Writing – review and editing (supporting). **Francesca Lioce**: Writing – original draft (supporting); Writing – review and editing (supporting). **Alexis Malagnino**: Writing – original draft (supporting); Writing – review and editing (supporting). **Christine Miller**: Writing – original draft (supporting); Writing – review and editing (supporting). **Wibke Peters**: Writing – original draft (supporting); Writing – review and editing (supporting). **Bostjan Pokorny**: Writing – original draft (supporting); Writing – review and editing (supporting). **Rudolf Reiner**: Writing – original draft (supporting); Writing – review and editing (supporting). **Andrea Rezić**: Writing – original draft (supporting); Writing – review and editing (supporting). **Sunčica Stipoljev**: Writing – original draft (supporting); Writing – review and editing (supporting). **Toni Tesija**: Writing – original draft (supporting); Writing – review and editing (supporting). **Yanko Yankov**: Writing – original draft (supporting); Writing – review and editing (supporting). **Tomasz Zwijacz-Kozica**: Writing – original draft (supporting); Writing – review and editing (supporting). **Nikica Sprem**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data is available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.fbg79cnx2>> (Corlatti et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Alzieu, J. P. et al. 2004. First description of pestivirus infection in *Rupicapra pyrenaica pyrenaica*. – Bull. Acad. Vet. France 157: 49–54.
- Anderwald, P. et al. 2021. *Rupicapra rupicapra* (amended version of 2020 assessment). – The IUCN Red List of Threatened Species 2021: e.T39255A195863093.
- Apollonio, M. et al. 2013. Consequences of snowy winters on male mating strategies and reproduction in a mountain ungulate. – Behav. Process. 98: 44–50.
- Apollonio, M. et al. 2020. Capital–income breeding in male ungulates: causes and consequences of strategy differences among species. – Front. Ecol. Evol. 8: 521767.
- Arnal, M. C. et al. 2004. A novel pestivirus associated with death in Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*). – J. Gen. Virol. 85: 3653–3657.
- Arnal, M. C. et al. 2013. Dynamics of an infectious keratoconjunctivitis outbreak by *Mycoplasma conjunctivae* on Pyrenean chamois *Rupicapra p. pyrenaica*. – PLoS One 8: e61887.
- Arnold, S. J. and Wade, M. J. 1984. On the measurement of natural and sexual selection: theory. – Evolution 38: 709–719.
- Bocci, A. et al. 2010. Even mortality patterns of the two sexes in a polygynous, near-monomorphic species: is there a flaw? – J. Zool. Lond. 280: 379–386.
- Brivio, F. et al. 2016. The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions. – Behav. Ecol. Sociobiol. 70: 1291–1304.
- Camerano, A. 1914. Ricerche intorno ai camosci (Parte Ia, IIa, IIIa). – Mem. della Regia Acc. Scienze Torino 64: 1–82, 64: 1–88, 65: 1–82.
- Chirichella, R. et al. 2013. Effects of livestock and non-native mouflon on use of high-elevation pastures by Alpine chamois. – Mamm. Biol. 78: 344–350.
- Chirichella, R. et al. 2021. Contrasting effects of climate change on Alpine chamois. – J. Wildl. Manage. 85: 109–120.
- Ciach, M. and Pełksa, L. 2019. Human-induced environmental changes influence habitat use by an ungulate over the long term. – Curr. Zool. 65: 129–137.
- Clauss, M. et al. 2009. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. – J. Morphol. 270: 929–942.
- Corlatti, L. et al. 2011. The conservation of the chamois *Rupicapra* spp. – Mamm. Rev. 41: 163–174.
- Corlatti, L. et al. 2012a. Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. – Anim. Behav. 84: 1061–1070.
- Corlatti, L. et al. 2012b. Unbiased sex-specific survival in Alpine chamois. – Mamm. Biol. 77: 135–139.

- Corlatti, L. et al. 2015a. Preliminary analysis of reproductive success in a large mammal with alternative mating tactics, the Northern chamois, *Rupicapra rupicapra*. – Biol. J. Linn. Soc. 116: 117–123.
- Corlatti, L. et al. 2015b. The use of block-counts, mark-resight and distance sampling to estimate population size of a mountain-dwelling ungulate. – Pop. Ecol. 57: 409–419.
- Corlatti, L. et al. 2017. Does selection on horn length of males and females differ in protected and hunted populations of a weakly dimorphic ungulate? – Ecol. Evol. 7: 3713–3723.
- Corlatti, L. et al. 2020. Weather stochasticity and alternative reproductive tactics in northern chamois, *Rupicapra rupicapra*. – Biol. J. Linn. Soc. 130: 359–364.
- Corlatti, L. et al. 2022a. Northern chamois *Rupicapra rupicapra* (Linnaeus, 1758) and southern chamois *Rupicapra pyrenaica* Bonaparte, 1845. – In: Corlatti, L. and Zachos, F. (eds), Handbook of the mammals of Europe – terrestrial cetartiodactyla. Springer Nature.
- Corlatti, L. et al. 2022b. Data from: Past, present and future of chamois science. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.fbg79cnx2>>.
- Couturier, M. 1938. Le Chamois. – Arthaud.
- Crestanello, B. et al. 2009. The genetic impact of translocations and habitat fragmentation in chamois (*Rupicapra* spp.). – J. Hered. 100: 691–708.
- Damm, G. and Franco, N. 2014. The CIC Caprinae Atlas of the World. – CIC International Council for Game and Wildlife Conservation, Budakeszi, Hungary in cooperation with Rowland Ward Publications RSA (Pty) Ltd.
- Degiorgis, M. P. et al. 2000. An outbreak of infectious keratoconjunctivitis in Alpine chamois (*Rupicapra r. rupicapra*) in Simmental-Gruyères, Switzerland. – Schweiz. Arch. Tierheilkd. 142: 520–527.
- Duparc, A. et al. 2020. Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes. – Oikos 129: 170–183.
- Espunyes, J. et al. 2019a. Seasonal diet composition of Pyrenean chamois is mainly shaped by primary production waves. – PLoS One 14: 1–23.
- Espunyes, J. et al. 2019b. Different effects of alpine woody plant expansion on domestic and wild ungulates. – Global Change Biol. 25: 1808–1819.
- Espunyes, J. et al. 2021. Positive effect of spring advance on diet quality of an alpine herbivore. – Integr. Zool. 17: 78–92.
- Fernandez, P. and Crégut, E. 2007. Les Caprinae (Rupicaprini, Ovibovini, Ovini et Caprini) de la séquence pléistocène de Kozarnika (Bulgarie du Nord): morphométrie, biochronologie et implications phylogéniques. – Rev. Paléobiol. Museum d'Hist. Nat. Ville Geneve 26: 425–503.
- Fernández-Aguilar, X. et al. 2017. Long-term dynamics of *Mycoplasma conjunctivae* at the wildlife-livestock interface in the Pyrenees. – PLoS One 12: e0186069.
- Fernández-Morán, J. et al. 1997. Epizootiology of sarcoptic mange in a population of cantabrian chamois (*Rupicapra pyrenaica parva*) in northwestern Spain. – Vet. Parasitol. 73: 163–171.
- Ferretti, F. et al. 2014. Males are faster foragers than females: intersexual differences of foraging behaviour in the Apennine chamois. – Behav. Ecol. Sociobiol. 68: 1335–1344.
- Ferretti, F. et al. 2015. Competition between wild herbivores: reintroduced red deer and Apennine chamois. – Behav. Ecol. 26: 550–559.
- Geist, V. 1987. On the evolution of the Caprinae. – In: Soma, H. (ed.), The biology and management of capricornis and related mountain antelopes. Croom Helm, pp. 3–40.
- Gelormini, G. et al. 2017. Infectious keratoconjunctivitis in wild Caprinae: merging field observations and molecular analyses sheds light on factors shaping outbreak dynamics. – BMC Vet. Res. 13: 67.
- Gilot-Fromont, E. et al. 2018. Self-clearance of pestivirus in a Pyrenean chamois (*Rupicapra pyrenaica*) population. – J. Wildl. Dis. 54: 335–341.
- Gonzalez, G. and Crampe, J.-P. 2001. Mortality patterns in a protected population of isards (*Rupicapra pyrenaica*). – Can. J. Zool. 79: 2072–2079.
- Grassi, L. et al. 2021. Ecotyping of *Anaplasma phagocytophilum* from wild ungulates and ticks shows circulation of zoonotic strains in northeastern Italy. – Animals 11: 310.
- Grattarola, C. et al. 1999. *Mycoplasma conjunctivae* infections in chamois and ibexes affected with infectious keratoconjunctivitis in the Italian Alps. – Vet. Rec. 145: 588–589.
- Hassanin, A. et al. 2009. Evolution of the mitochondrial genome in mammals living at high altitude: new insights from a study of the tribe Caprini (Bovidae, Antilopinae). – J. Mol. Evol. 68: 293–310.
- Hauffe, H. C. and Barelli, C. 2019. Conserve the germs: the gut microbiota and adaptive potential. – Conserv. Genet. 20: 19–27.
- Herrero, J. et al. 2020. *Rupicapra pyrenaica*. – The IUCN Red List of Threatened Species 2020: e.T19771A171131310.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – Oecologia 78: 443–457.
- Hurtado, A. et al. 2004. Molecular identification of a new pestivirus associated with increased mortality in the Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) in Spain. – J. Wildl. Dis. 40: 796–800.
- Iacolina, L. et al. 2019. Hybridisation in European ungulates: an overview of the current status, causes and consequences. – Mamm. Rev. 49: 45–59.
- Iacolina, L. et al. 2021. A mother's story, mitogenome relationships in the genus *Rupicapra*. – Animals 11: 1065.
- Kavčić, K. et al. 2021a. Rutting behavior of male Balkan chamois. – Mamm. Biol. 101: 895–905.
- Kavčić, K. et al. 2021b. Random encounter model to estimate density of mountain-dwelling ungulate. – Eur. J. Wildl. Res. 67: 87.
- Krämer, A. 1969. Soziale organisation und sozialverhalten einer gemspopulation (*Rupicapra rupicapra* L.) der Alpen. – Z. Tierpsychol. 26: 890–964.
- Kupferschmid, A. et al. 2014. Light availability and ungulate browsing determine growth, height and mortality of *Abies alba* saplings. – For. Ecol. Manage. 318: 359–369.
- Loison, A. et al. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. – Ecology 80: 2539–2554.
- Lovari, S. et al. 2006. Do alternative strategies of space use occur in male Alpine chamois? – Ethol. Ecol. Evol. 18: 221–231.
- Lovari, S. et al. 2020. Climatic changes and the fate of mountain herbivores. – Clim. Change 162: 2319–2337.
- Lovari, S. and Scala, C. 1980. Revision of *Rupicapra* genus. I. A statistical re-evaluation of Couturier's data on the morphometry of six chamois subspecies. – Boll. Zool. 47: 113–124.
- Luzzago, C. et al. 2016. Spatial and temporal phylogeny of border disease virus in Pyrenean chamois (*Rupicapra p. pyrenaica*). – PLoS One 11: e0168232.

- Masini, F. and Lovari, S. 1988. Systematics, phylogenetic relationships and dispersal of the chamois, *Rupicapra* spp. – *Quat. Res.* 30: 339–349.
- Mason, T. H. et al. 2011. Contrasting life histories in neighbouring populations of a large mammal. – *PLoS One* 6: e28002.
- Mason, T. H. et al. 2014. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. – *Global Change Biol.* 20: 3872–3882.
- Molinari-Jobin, A. et al. 2007. Variation in diet, prey selectivity and home-range size of Eurasian lynx *Lynx lynx* in Switzerland. – *Wildl. Biol.* 13: 393–405.
- Mori, E. et al. 2017. What does the wild boar mean to the wolf? – *Eur. J. Wildl. Res.* 63: 1–5.
- Nascetti, G. et al. 1985. Revision of *Rupicapra* genus, III. Electrophoretic studies demonstrating species distinction of chamois populations of the Alps from those of the Apennines and Pyrenees. – In: Lovari, S. (ed.), *The biology and management of mountain ungulates*. Croom-Helm, pp. 56–62.
- Nopp-Mayr, U. et al. 2020. Analyzing long-term impacts of ungulate herbivory on forest-recruitment dynamics at community and species level contrasting tree densities versus maximum heights. – *Sci. Rep.* 10: 20274.
- Pérez, T. et al. 2014. Biogeography of chamois: What different molecular markers can tell us. – In: Antonucci, A. and Di Domenico, G. (eds), *Chamois international congress proceedings, 17–19 June 2014, Lama dei Peligni, Majella National Park, Italy*, pp. 71–75.
- Pérez, T. et al. 2017. Multilocus intron trees reveal extensive male-biased homogenization of ancient populations of chamois (*Rupicapra* spp.) across Europe during late Pleistocene. – *PLoS One* 12: e0170392.
- Reiner, R. et al. 2020. Deterministic reconstruction as an informative tool for monitoring chamois populations. – *Wildl. Biol.* 2020: wlb.00757.
- Reiner, R. et al. 2021. Forests buffer the climate-induced decline of body mass in a mountain herbivore. – *Global Change Biol.* 27: 3741–3752.
- Rivals, F. 2004. Les petits bovidés (Caprini et rupicaprini) pléistocènes dans le bassin méditerranéen et le Caucase: étude paléontologique, biostratigraphique, archéozoologique et paléocologique. – *Brit. Archaeol. Rep.* 1327: 1–252.
- Rodríguez, F. et al. 2009. Cytochrome b phylogeography of chamois (*Rupicapra* spp.). Population contractions, expansions and hybridizations governed the diversification of the genus. – *J. Hered.* 100: 47–55.
- Rossi, L. et al. 1995. The epizootiology of sarcoptic mange in chamois, *Rupicapra rupicapra*, from the Italian eastern Alps. – *Parasitologia* 37: 233–240.
- Rughetti, M. and Festa-Bianchet, M. 2010. Compensatory growth limits opportunities for artificial selection in Alpine chamois. – *J. Wildl. Manage.* 74: 1024–1029.
- Rughetti, M. and Festa-Bianchet, M. 2011. Seasonal changes in sexual size dimorphism in northern chamois. – *J. Zool.* 284: 257–264.
- Schaller, G. B. 1977. *Mountain monarchs: wild sheep and goats of the Himalaya*. – Chicago Univ. Press.
- Schröder, W. 1971. Untersuchungen zur Ökologie des Gamswildes (*Rupicapra rupicapra* L.) in einem Vorkommen der Alpen – I. teil. – *Z. Jagdwiss.* 17: 113–168.
- Senf, C. and Seidl, R. 2021. Mapping the forest disturbance regimes of Europe. – *Nat. Sustain.* 4: 63–70.
- Serrano, E. et al. 2015. Border disease virus: an exceptional driver of chamois populations among other threats. – *Front. Microbiol.* 6: 1307.
- Shackleton, D. M. (ed.) 1997. *Wild Sheep and Goats and their Relatives. Status survey and Conservation Action Plan for Caprinae*. IUCN, Gland, Switzerland and Cambridge, UK.
- Simpson, G. C. 1945. The principles of classification and a classification of mammals. – *Bull. Am. Museum Nat. Hist.* 85: 1–350.
- Skonhøft, A. et al. 2002. Management of chamois (*Rupicapra rupicapra*) moving between a protected core area and a hunting area. – *Ecol. Appl.* 12: 1199–1211.
- Tettamanti, F. et al. 2015. Senescence in breeding success of female Alpine chamois (*Rupicapra rupicapra*): the role of female quality and age. – *Oecologia* 178: 187–195.
- Thirgood, S. J. 1991. Alternative mating strategies and reproductive success in fallow deer. – *Behaviour* 116: 1–10.
- Vavra, M. and Riggs, R. A. 2010. Managing multi-ungulate systems in disturbance-adapted forest ecosystems in North America. – *Int. J. For. Res.* 83: 177–187.
- Vitasse, Y. et al. 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. – *Biol. Rev.* 96: 1816–1835.
- von Hardenberg, A. et al. 2000. Male Alpine chamois occupy territories at hotspots before the mating season. – *Ethology* 106: 617–630.
- Yankov, Y. 2021. New data about parasitological status of Balkan chamois at three mountains in Bulgaria. – In: *Proc. 3rd Int. Rupicapra Symp., Makarska, 16–18 June*, pp. 54–55.